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ELLOBIOPSIDAE

by

Dr H. Boschma, F.M.L.S., C.M.Z.S.

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Dr H. BOSCHMA, F.M.L.S., C.M.Z.S.

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ELLOBIOPSIDAE

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(Plates XXXVIII–XLI; Text-figs. 1–16)

INTRODUCTION

THE material of the parasitic Protozoa, Ellobiopsidae, in the Discovery collections is interesting, as it contains specimens of three of the larger species of the family, all belonging to the genus *Amallocystis*. As the material was in an excellent state of preservation, a comparative study could be made of the organ of fixation and the parts of the organism which obviously serve for the absorption of food. The rather complicated structure of these parts in two of the species found its explanation in the more simple arrangement occurring in the third species.

The collection contains abundant material of a parasite of various Euphausiacea, described in a short preliminary note (Boschma, 1948) as *A. fagei*. There are previous records of this species, but until recently it remained unnamed.

The new species *A. umbellatus* described in the present paper is the first of the genus to become known as a parasite of Caridea of the family Hoplophoridae. In the collection there are two specimens, one of which was studied in more detail.

Finally, the collection contains two specimens of *A. capillosus* Fage, a parasite of Caridea of the genus *Pasiphaea*, hitherto known from the Skagerrak only. The specimens described here are from the Strait of Magellan.

I am much obliged to Dr L. B. Holthuis for determining the sex of the specimens of *Hoplophorus* and of *Pasiphaea* infested with *Amallocystis*. Moreover, I am much indebted to Dr N. A. Mackintosh for his care in editing the present paper.

REVIEW OF THE LITERATURE OF THE ELLOBIOPSIDAE

Sars (1868). Description and figure of parasitic bodies on the third maxillipede and the two preceding appendages of *Pasiphaea multidentata* Esmark (*P. norvegica* M. Sars). Their shape was reminiscent of the Gregarinids; the smaller specimens consisted of a cylindrical sac with rounded free extremity, and the larger specimens consisted of two sacs, one on the top of the other. The distal sac was smaller and thinner than the proximal, the latter often being thicker in its upper than in its lower part. It is not improbable that these parasitic bodies were Ellobiopsidae consisting of a trophomere which could give rise to one gonomere. They remind one of *Ellobiocystis tenuis* Coutière, 1911*c*, parasitic on *Pasiphaea sivado* (Risso).

Bate (1888). To the description of his new species *P. cristata* from St. 173 of the Challenger Expedition (off the Fiji Islands, 315 fathoms) this author adds: 'In our specimen, which I consider to be a female, there is a mass of parasitic cell-growth (fig. 3) strung together in a bead-like arrangement and suspended from a common centre' (loc. cit., p. 869). The figures (loc. cit., pl. cxl, figs. 1, 3 and 3′) show that the parasite is attached to the ventral surface of the second abdominal segment; it consists of groups of trophomeres, each bearing two or three gonomeres. In the most highly enlarged figure there are visible the remains of recently detached gonomeres.

Scott (1897). Drawing of a specimen of *Calanus finmarchicus* (Gunn.) found in the Clyde, up as far as the head of Loch Fyne, with an 'Infusorian-like' parasite. The author adds: 'the parasites are found adhering to the body of the copepods, to the antennules, to the antennae, and to other appendages, but usually about the head; sometimes large numbers of *Calanus* will be found infested by these parasites.' The figure shows a parasite with a comparatively long stalk. The body is divided into a smaller proximal part and a larger distal part, just as in *Ellobiopsis chattoni* described by Caullery (1910).

Mrázek (1902). Numerous specimens of *Calanus finmarchicus* from the Spitzbergen region of the Arctic Sea showed large short-stalked 'cysts of some Ciliate' on the antennulae or on the maxillipedes or on the thorax. Mrázek was convinced that these cysts were the same as the parasites mentioned and figured by Scott (1897).

Caullery (1910). Description of *Ellobiopsis chattoni*, a parasite of *Calanus helgolandicus* Claus from Banyuls-sur-mer. The parasites are attached by means of a stalk to the mouthparts, maxillipedes, and antennae of the copepod. Young stages are oval or globular; older stages show a division of the body in two parts, a smaller trophomere and a larger gonomere. The stalk penetrates into the appendage of the host. Caullery is convinced that this stalk is not only an organ of fixation, but also an organ for the absorption of food from the host. The systematic position of the parasite is discussed, and there are indications which point to its being allied to the Peridinians, which are known to contain a number of parasitic forms. In a postscript Caullery adds that Mrázek drew his attention to the similarity of *Ellobiopsis* to the parasites mentioned by Scott (1897). Material afterwards received from Scott proved the identity of the two forms.

Apstein (1911). Notes on 'Parasit 19' occurring on *Pseudocalanus*, *Calanus* and *Acartia*; as a rule on the antennae. The figures represent one undivided specimen and one with distinct trophomere and gonomere. The more or less globular gonomere is about half as large as the slightly elongate trophomere.

Coutière (1911*a*). Short description of parasites occurring on *Parapasiphaë grimaldii* Coutière (not mentioned in later papers by the same author as a host of Ellobiopsidae), *Acanthephyra purpurea* A.M.E. and *A. pulchra* A.M.E., similar to *Ellobiopsis chattoni* Caullery. These parasites do not show a transverse septum (no division in trophomere and gonomere); they are attached to their hosts by simple broadening of their proximal extremity, without penetrating the appendage of the host.

Coutière (1911*b*). Remarks that specimens of *Ellobiopsis* were found by him on *Systellaspis debilis* (A.M.E.), *Acanthephyra pulchra* A.M.E. and *A. purpurea* A.M.E. To these parasites the common name *Ellobiopsis caridarum* is given, though there are five forms of probably specific distinction. The most common form, indicated as α, is ovoid or elongate, without stalk; β is a swollen form with a long stalk originating from a broad circular base; γ is a slightly conical form with broad base of attachment, and its cuticle is covered with soft hairs; ϵ is a form consisting of two successive cylindrical elements; η is a form with short spherical elements. Consequently in ϵ and η the body is divided into trophomere and gonomere, whereas in the other forms no such division was observed.

In the same paper an Ellobiopsid is described consisting of about fifty cylindrical bodies, united on a common stalk, the cylindrical bodies up to 4 mm. long, each divided into two to eight elements. The stalk penetrates the abdominal wall of the host, *Pasiphaea tarda* Kröyer, and ends with a blunt point in the connective tissue under the ventral nerve cord. Coutière names this organism, which he regards as a real parasite, *Ellobiopsis racemosus*.

Chatton (1911). Points to the similarity of Apstein's parasite 19 with *E. chattoni* Caullery and the parasite found by Scott on *Calanus finmarchicus* (Gunn.).

Coutière (1911*c*). More elaborate data on the Ellobiopsidae dealt with in previous papers (Coutière,

1911*a*, *b*). Genus *Staphylocystis*, type *Ellobiopsis racemosus* Coutière; genus *Ellobiocystis*, type *Ellobiopsis caridarum* Coutière. The author distinguishes the following species:

Staphylocystis racemosus, on the ventral surface of the third abdominal segment of *Pasiphaea tarda* Kröyer, from St. 1038 of the cruises of the 'Princesse-Alice', north-east of Iceland, 3310 m. According to Coutière the parasite described by Bate on *P. cristata* Bate from the Fiji Islands belongs to this species.

In the genus *Ellobiocystis* Coutière recognizes a number of species. The hosts were collected during the cruises of the 'Princesse-Alice' in the region of the Bay of Biscay to the Azores from depths up to 5000 m. (except *E. mysidarum*). The species chiefly occur on the mouthparts and the maxillipedes of the hosts. The names given by Coutière are:

Ellobiocystis caridarum, on *Acanthephyra purpurea* A.M.E., *A. pulchra* A.M.E. and *Systellaspis debilis* (A.M.E.).

Ellobiocystis villosus (forme γ of 1911*b*), on *Acanthephyra purpurea* A.M.E.

Ellobiocystis tuberosus (forme η of 1911*b*), on *Acanthephyra purpurea* A.M.E.

Ellobiocystis filicollis (forme β of 1911*b*), on *Acanthephyra purpurea* A.M.E.

Ellobiocystis catenatus (forme ϵ partim of 1911*b*), on *Acanthephyra purpurea* A.M.E.

Ellobiocystis tenuis (forme ϵ partim of 1911*b*), on *Pasiphaea sivado* (Risso).

Ellobiocystis mysidarum, on *Antarctomysis maxima* (H. J. Hansen, MS. in Holt and Tattersall) from the Antarctic (the French Antarctic Expedition of the 'Pourquoi-Pas?').

Finally, Coutière mentions small parasites of *Sergestes* sp., from the cruises of the 'Princesse-Alice', in all probability belonging to *Ellobiocystis caridarum*.

Caullery (1912). Short note on the particulars and the systematic position of *Ellobiopsis chattoni*, abstract of a paper read at the Congress of Zoology of 1910.

Lühe (1912). In the discussion following the paper by Caullery, Lühe remarked that he had found on the gills of a Unionid parasites which were extraordinarily similar to those described by Caullery. No further data being available, it is impossible to decide whether or not these parasites belonged to the Ellobiopsidae.

Collin (1913). Description of *Parallobiopsis coutieri*, parasite of *Nebalia bipes* (O. Fabr.). The parasite is attached to the abdominal appendages, the gills, and especially to the membranous folds of the cephalothorax of the host. It is fixed to the chitin by a circular sucker, and according to Collin it has no root system ('il n'émet point de rhizoïdes'). In young stages the body already shows a transverse septum; in older stages up to nine successive gonomeres may be observed, and the topmost may show the remnants of a former gonomere from which the spores have escaped.

Chatton (1920). This extensive paper was completed in May 1914; it gives, besides data on real parasitic Peridinea, the most important particulars of the Ellobiopsidae. Concerning the species distinguished by Coutière in his genus *Ellobiocystis*, Chatton remarks that a specimen of *E. caridarum* (Coutière, 1911*c*, pl. viii, fig. 18) in its lower half shows hairs, as they occur as a specific character in *E. villosus*. This causes some doubt concerning the specific status of the various forms.

Willey (1920). Figure and notes of a 'two-chambered cyst' attached to the right antenna of a female of *Pseudocalanus elongatus* (Boeck) from Collinson point (Camden bay), Arctic Alaska, 1–2 fathoms, similar to the parasites observed by Scott (1897), now named *Ellobiopsis chattoni* Caullery. In the trophomere and in the gonomere a faint indication of a radial arrangement of the contents was observed. The shape of Willey's specimen differs from Caullery's specimens of *E. chattoni* in so far as the more or less conical trophomere is much larger than the globular gonomere.

Zachs (1923). Description and figure of *E.* (?) *eupraxiae* on the parapodia of the Polychaete worm *Nephthys ciliata* Müller from the White Sea. The parasite consists of an elongately oval trophomere and

one to five globular gonomeres. In the figured specimen spores are emerging from the top of the distal gonomere. The parasite penetrates into the host by means of a more or less dichotomously divided root system.

Hovasse (1925*a*). The spores of *Parallobiopsis coutieri* Collin are flagellispores, not dinospores as might have been expected on the presumption that the Ellobiopsidae are allied to the Peridinea.

Hovasse (1925*b*). Cytological studies of the cycle of evolution of *P. coutieri*.

Hovasse (1926). Extensive studies of living and preserved material of *P. coutieri*. The author shows that this organism is a real parasite, as in the centre of the sucker with which it is attached to the host the cuticle of the latter shows an opening through which a protoplasmatic mass of the parasite penetrates into the tissues underlying the cuticle, thereby forming an organ for the absorption of food. As far as concerns the systematic position of the Ellobiopsidae, Hovasse remarks that they form a special group in the class Flagellata. The form described by Zachs as *Ellobiopsis eupraxiae*, according to Hovasse must be the type of a separate genus, on account of its divided root system. Hovasse proposes for this genus the name *Rhizellobiopsis*; he remarks that the shape of this parasite corresponds with *Staphylocystis* in so far as it bears more than one gonomere on the top of its trophomeres.

Macdonald (1927). Among the parasites of *Meganyctiphanes norvegica* (M. Sars) this author notes: '*Staphylocystis racemosus* (Coutière), a dinoflagellate found on the carapace of a specimen caught at "Cumbrae Deep" in March 1925. The only record of this parasite is that of Kröyer on *Pasiphaea tarda* in N.E. Iceland' (loc. cit., p. 780). Instead of 'Kröyer', read 'Coutière'; the type specimen of Coutière's *Staphylocystis racemosus* is from north-east Iceland. In all probability, however, the identification of the parasite is incorrect. It is stated to occur 'on the carapace', and, therefore, almost certainly belongs to *Amallocystis fagei* dealt with in the present paper. Support to this opinion is, moreover, given by the fact that the host is a Euphausiid. The hitherto known Ellobiopsidae of this group of Crustacea belong to the species *A. fagei*.

Steuer (1928). Notes on *Ellobiopsis chattoni* as a parasite of the copepods *Pleuromamma gracilis* (Claus) from one station in the Indian Ocean, about half-way between south India and Madagascar, and of *P. borealis* (F. Dahl) from two stations in the South Atlantic, off South Africa. The material was obtained by the Valdivia Expedition, from depths of 2000–2500 m. Young and older stages of the parasite are described and figured. The adult stage differs from the specimens of *Ellobiopsis chattoni* described by Caullery (1910) in being smaller (422μ against 700μ), and in having a different shape. In Caullery's specimens the gonomere is much larger than the trophomere, in Steuer's figure the globular gonomere is much smaller than the pear-shaped trophomere. Moreover, the groove between the two parts of the parasite in Steuer's specimen is much more pronounced than in those of Caullery. Steuer classifies the Ellobiopsidae among the Flagellata.

Reichenow (1930). *Ellobiopsis chattoni* recorded as occurring in the North Sea and in the Baltic. Notes on the distribution of the other Ellobiopsidae.

Steuer (1932*a*). Description of *E. elongata*, a parasite of *Ctenocalanus vanus* Giesbr. from the Meteor Expedition (St. 57, about 50° S, 35° W, near South Georgia, from a depth of 50–100 m.). Differs from *Ellobiopsis chattoni* by its more slender, cylindrical trophomeres, which in full-grown specimens bear two globular gonomeres. The stalk penetrates into the appendage of the host.

Steuer (1932*b*). More elaborate notes on the specimens of *E. chattoni* dealt with in a previous paper (Steuer, 1928), with three more records of the parasite in the Indian Ocean (stations of the Valdivia Expedition) and one more record in the Atlantic, off South Africa (station of the Meteor Expedition). A map shows the distribution of *E. chattoni*, based on the data in Steuer's paper and in those from the previous literature.

Steuer (1933). A summary of the 1932*b* paper by the same author.

Marshall, Nicholls and Orr (1934). Note on the occurrence of *E. chattoni* on *Calanus finmarchicus* in Loch Striven (Firth of Clyde area).

Fage (1936). New generic name *Amallocystis* for *Staphylocystis*, preoccupied. Description of *Amallocystis fasciatus*, a parasite on the ventral side of the first abdominal segment of *Gnathophausia zoea* Will. S. (Mysidacea) from the Dana Expedition (off the Fiji Islands and off New Zealand, 3000 and 2500 m. wire respectively). Fage describes the characters separating the species from *Amallocystis racemosus* (Coutière), gives an account of the organ of fixation, and notes on cytology, and refers to the influence of the parasite on the host. One of the hosts, a male, does not appear to have undergone any change as a result of being infested by the parasite. On the contrary the other host, a female, shows a pronounced retardation in the development of the sexual characters. The oostegites of the parasitized female are considerably smaller than those of uninfested females of the same size, and the mass of hairs found on the sternal plates of normal females has remained very much under-developed in the specimen bearing the parasite.

Jepps (1937). Notes on young and adult stages of *Ellobiopsis chattoni* attached to the mouthparts and the second antenna of *Calanus helgolandicus* Claus from the Clyde Sea area, and on very young stages of the parasite attached to the setae of the appendages. The larger specimens showed well-developed roots penetrating into the appendages of the copepod. In some of the gonomeres the formation of buds leading to sporulation was observed. A plug and an anterior cone are described as often occurring on the top of the gonomere; these might be the remnants of a previous gonomere, detached from the trophomere before the present gonomere developed.

Fage (1938). Description of *Amallocystis capillosus*, a parasite of *Pasiphaea tarda* Kröyer from the Skagerrak. The external parts of the parasite form two tufts of long-stalked trophomeres, each tuft on one side of the base of the rostrum. The basal part of each tuft passes through a hole in the cuticle into the internal part of the parasite, forming the organ of fixation, which extends transversely under the rostrum of the host. This internal part has a rough surface. Fage remarks that the simple Ellobiopsidae, which may be found in various parts of their hosts, in all probability attain their full development on the spot where the spore originally attached itself. For the compound Ellobiopsidae, each species of which occurs in a definitely localized part of its host, it is hardly possible to believe that they originally fixed themselves on the spot. In connexion with this Fage points to the probability that in the life history of these parasites there occurs an internal stage.

Coutière (1938, 1940*a*, *b*). Reprinted previous papers by the same author (Coutière, 1911*a–c*).

Fage (1941). Data from a previous paper (Fage, 1936) with additional notes. *Amallocystis fasciatus* on a third specimen of *Gnathophausia zoea* (from off Guyana), and on two specimens of *G. ingens* (Dohrn), one from the Indian Ocean, the other from the Atlantic.

Fage (1942). Notes on the effect of the parasite *Amallocystis fasciatus* on its hosts.

Einarsson (1945). Remarks on *Amallocystis* sp., a parasite of the Euphausiids *Thysanoessa inermis* (Kröyer) and *Th. raschii* (M. Sars) from Icelandic waters. The parasite occurs on the carapace of the host, as a rule in the region of the genital gland, and in some cases in the region of the stomach. Often more than one parasite on one host. Description of the root system extending from the organ of fixation into the ovary of the host. The parasite seems to castrate the animals which it infests, as external sexual characters are totally absent and the ovary is completely disorganized in the specimens bearing the parasites.

Boschma (1948). Description of *Amallocystis fagei*, a parasite of *Euphausia vallentini* Stebbing and other Euphausiids not mentioned by name (material from various Discovery Stations in the Antarctic), with an account of the sieve plate occurring in the organ of fixation.

Amallocystis fagei Boschma

Staphylocystis racemosus Macdonald, 1927, p. 780.
Amallocystis sp. Einarsson, 1945, p. 158.
Amallocystis fagei Boschma, 1948, p. 448.

MATERIAL:

St. 665 (51° 41′ 30″ S, 29° 58′ 45″ W), 17. iv. 1931, net TYFB, depth of net 250–0 m., 1 ex. on *Euphausia frigida* H. J. Hansen. Transverse sections of host, Delafield's haematoxylin (Fig. 3*b*).

St. WS 770 (46° 03′ S, 66° 34′ W), 21. x. 1931, net N 100 B, depth of net 57–0 m., 6 ex. on *Euphausia vallentini* Stebbing. Three specimens figured in Pl. XXXVIII, figs. 1–5, 10; one specimen transverse sections of host, Ehrlich's haematoxylin (Pl. XXXIX); one specimen longitudinal sections of host, Delafield's haematoxylin (Pl. XL).

St. 712 (28° 02′ 06″ S, 43° 09′ 30″ W), 28. x. 1931, net TYFB, depth of net 224–0 m., 1 ex. on *Euphausia recurva* H. J. Hansen (Pl. XXXVIII, fig. 6).

St. 733 (62° 56′ 42″ S, 75° 02′ W), 21. xi. 1931, net N 100 B, depth of net 84–0 m., 1 ex. on *Euphausia frigida* H. J. Hansen.

St. 748 (55° 29′ 24″ S, 54° 13′ 48″ W), 29. xi. 1931, net N 100 B, depth of net 180–0 m., 1 ex. on *Euphausia frigida* H. J. Hansen.

St. 751 (51° 28′ 42″ S, 49° 17′ 42″ W), 1. xii. 1931, net N 100 B, depth of net 104–0 m., 2 ex. on *Euphausia frigida* H. J. Hansen. One specimen figured in Pl. XXXVIII, figs. 8 and 11; one specimen longitudinal sections of host, Ehrlich's haematoxylin (Fig. 4).

St. 766 (58° 51′ S, 36° 54′ W), 10. xii. 1931, net N 100 B, depth of net 102–0 m., 1 ex. on *Euphausia frigida* H. J. Hansen. Transverse sections of host, Delafield's haematoxylin (Fig. 3*a*).

St. 869 (43° 56′ 30″ S, 103° 24′ 18″ E), 5. v. 1932, net N 100 B, depth of net 68–0 m., 1 ex. on *Euphausia lucens* H. J. Hansen.

St. 871 (39° 32′ 06″ S, 107° 06′ 24″ E), 7. v. 1932, net N 100 B, depth of net 240–100 m., 1 ex. on *Thysanoessa gregaria* G. O. Sars. Transverse sections of host, Ehrlich's haematoxylin (Fig. 5).

St. 872 (37° 09′ 06″ S, 108° 47′ 12″ E), 7. v. 1932, net N 100 B, depth of net 128–0 m., 1 ex. on *Euphausia hemigibba* H. J. Hansen (Pl. XXXVIII, fig. 9).

St. 892 (52° 48′ 30″ S, 137° 00′ 24″ E), 31. v. 1932, net N 100 B, depth of net 93–0 m., 1 ex. on *Euphausia vallentini* Stebbing. Transverse sections of host, borax carmine (Fig. 2).

St. 963 (52° 01′ S, 139° 13′ 12″ W), 14. ix. 1932, net N 100 B, depth of net 320–128 m., 1 ex. on *Euphausia vallentini* Stebbing. Type specimen, transverse sections of host, Delafield's haematoxylin (Figs. 1, 9*b*).

St. 965 (47° 16′ 54″ S, 132° 25′ 06″ W), 16. ix. 1932, net N 100 B, depth of net 310–132 m., 1 ex. on *Thysanoessa gregaria* G. O. Sars (Pl. XXXVIII, fig. 7).

St. 1056 (50° 18′ S, 37° 04′ 30″ W), 4. xii. 1932, net N 100 B, depth of net 100–0 m., 1 ex. on *Euphausia vallentini* Stebbing.

The first record of this parasite undoubtedly is the specimen on *Meganyctiphanes norvegica* (M. Sars) identified by Macdonald (1927) as *Staphylocystis racemosus* (Coutière). As the author states that the parasite occurred on the carapace of this host, and as the host belongs to the Euphausiacea, it cannot have been the species of Coutière which lives on the underside of the abdomen of a host belonging to the Caridea.

More particulars on the parasite of the Euphausiids are given by Einarsson (1945). This author states that the parasite is closely allied to *Amallocystis racemosus* (Coutière), *A. fasciatus* Fage and *A. capillosus* Fage, and remarks that most probably it is a species new to science, which he provisionally indicates as *Amallocystis* sp. Einarsson states that this parasite, which he found on *Thysanoessa inermis* and *Th. raschii*, is always attached to the dorsal side of the carapace, usually in the middle or behind the middle, but in rare cases in the region of the stomach. Interesting is the following remark (Einarsson, 1945, p. 158): 'Usually there are more than one bundle of trophomeres and gonomeres present, most often three or more, which seem to have no connection with each other.' This points to the fact that in the North Atlantic, specimens of *Thysanoessa* may be infested by a number of separate individuals of the parasite.

Einarsson's fig. 81 distinctly shows that his parasite corresponds with those dealt with in the present paper. His figures of transverse sections of a specimen of *Thysanoessa* with *Amallocystis* sp. (loc. cit., fig. 83*b*, *c*) show the organ of fixation in its most strongly developed region, and the ramifications of the

parasite inside the ovary (referred to in the present paper as 'protoplasmatic excrescences' or 'root system'). Einarsson describes the chief particulars of the internal part of the parasite: 'The stalk of the parasite, which penetrates the carapace, may be followed in the sections, often dividing into branches which run horizontally through the internal organs, but sometimes it is confined to one strong continuation of the stalk' (loc. cit., p. 158). In the infested specimens of *Thysanoessa* Einarsson found that the external sexual characters are totally absent; it therefore seemed probable that the parasite castrates its host. Examination of sections of the ovary of a mature female and of an infested specimen showed that in the latter the ovary was completely disorganized.

Recently I published a short paper on the organs of absorption in a species of *Amallocystis* (Boschma, 1948), a preliminary communication dealing with a part of the material from the Discovery collections. The parasites of the Euphausiids were mentioned here as *A. fagei*; provisionally the peculiar manner of attachment to the region of the genital gland of the host was considered as a sufficient indication of its specific distinction. In this paper I mentioned protoplasmatic excrescences penetrating from the organ of fixation into the ovary (at the time I did not know that Einarsson already had described these prolongations of the organ of fixation), and showed that the cuticle of the organ of fixation possesses a distinct sieve plate through which the protoplasmatic excrescences protrude. Fage (1936) already had given as his opinion that the organ of fixation of *Amallocystis* not only serves as a means of attachment of the parasite, but that it also functions as an organ of absorption of food. After having found the sieve plate and the protoplasmatic excrescences emerging through this plate into the ovary I concluded that these are the real organs for the absorption of food; the cuticle of the organ of fixation itself is too thick to allow the passage of food.

A more detailed description of the Discovery material follows here.

The parasites are found slightly behind the middle of the dorsal surface of the carapace of the host. Their external part consists of a bundle of cylindrical bodies which are divided into a series of elements by distinct transverse grooves. On the larger specimens of the Euphausiids the parasites may show a considerable number of these cylindrical bodies; in one specimen on *Euphausia vallentini* (Pl. XXXVIII, figs. 1, 4) fifty of them could be counted. As a rule, however, this number in the parasites on *E. vallentini* does not exceed thirty (as in the specimen in Pl. XXXVIII, figs. 2, 5). The parasites of *E. frigida* have approximately the same number of cylindrical bodies (Pl. XXXVIII, fig. 8). On the parasites of *E. recurva* (Pl. XXXVIII, fig. 6), *E. lucens*, *E. hemigibba* (Pl. XXXVIII, fig. 9), and *Thysanoessa gregaria* (Pl. XXXVIII, fig. 7) ten to fifteen of these cylindrical bodies were counted.

The cylindrical bodies vary in length from 0·5 to 2·5 mm., and their transverse diameter is from 0·13 to 0·33 mm. They consist of up to eight elements, the proximal of which, the trophomere, is more or less conical, whilst the others, the gonomeres, have a more or less globular shape. The distal gonomere may grow out into a more elongated body (some of these are visible in Pl. XXXVIII, figs. 1, 4), which may easily break off from the top. The following gonomere then may show a distinct scar (visible in some of the gonomeres of Pl. XXXVIII, figs. 2, 10). Probably, however, this is not the natural manner of detachment of the ripe gonomeres. Numerous distal gonomeres show at their free extremities a kind of filament (distinctly visible in Pl. XXXVIII, figs. 8, 11), which consists of the shrivelled cuticle of the preceding gonomere from which apparently the spores have been set free.

As a rule the parasites of large specimens of the host are pronouncedly larger than those infesting smaller specimens of the host. Measurements of the transverse diameter of the gonomeres of various specimens yielded the following results. Two specimens on *Euphausia vallentini*, gonomeres 0·28–0·33 mm.; one specimen on *E. frigida*, gonomeres 0·28–0·33 mm.; another specimen on *E. frigida*, gonomeres 0·16–0·23 mm.; specimens on *E. hemigibba* and on *E. recurva*, gonomeres 0·13–0·16 mm.; specimen on *Thysanoessa gregaria*, gonomeres 0·13–0·16 mm.

The internal parts of the parasites were studied in sections. Six hosts with parasites were sectioned transversely and two longitudinally. In one of the latter the host proved to be infested by two parasites. The chief particulars of the various series of sections are given below.

(1) The type specimen, on *Euphausia vallentini* from St. 963 (Fig. 1). The section shows the external part of the organ of fixation from which a number of trophomeres are branching off, and the internal

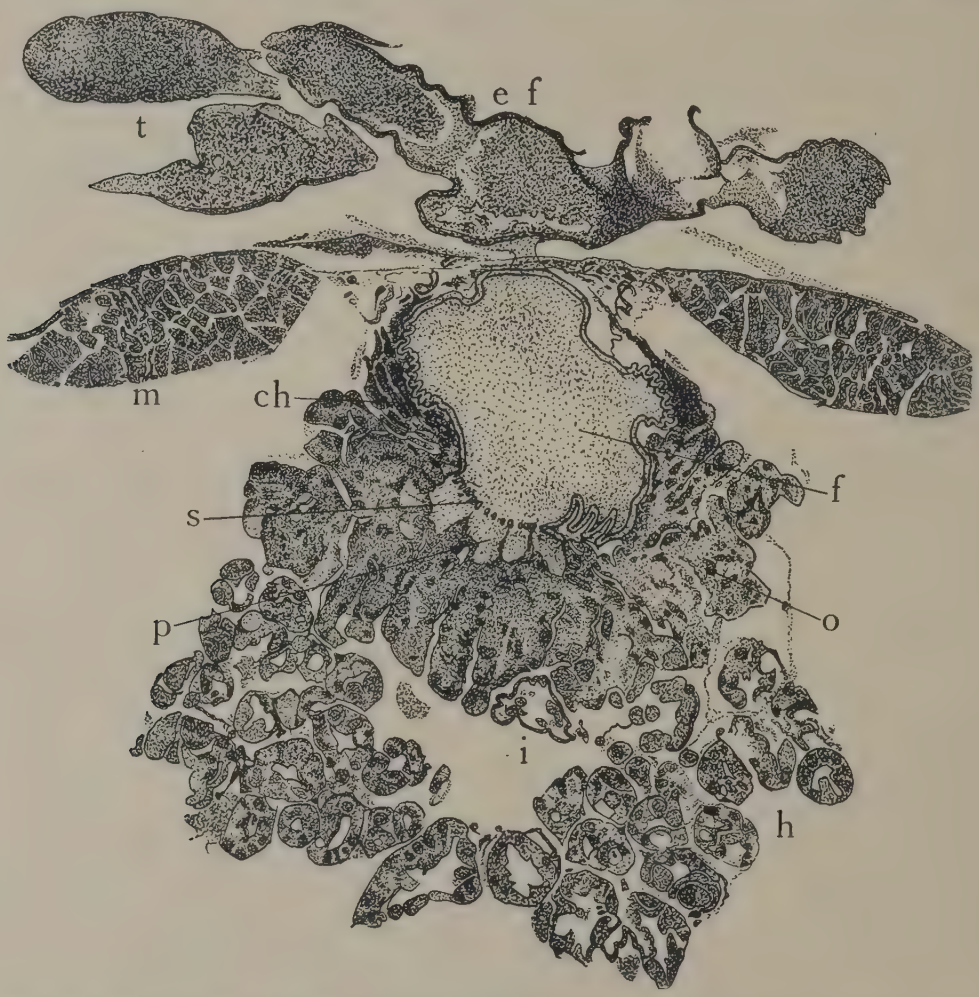

Fig. 1. *Amallocystis fagei* Boschma on *Euphausia vallentini* Stebbing from St. 963 (type specimen). Transverse section of host. After Boschma (1948, fig. 2). *ch*, chitin; *e f*, external part of organ of fixation; *f*, organ of fixation; *h*, hepatopancreas of host; *i*, intestine of host; *m*, musculature of host; *o*, ovary of host; *p*, protoplasmatic excrescences; *s*, sieve plate; *t*, trophomere. × 160.

part of the organ of fixation embedded in the ovary of the host. The organ of fixation has a rather solid cuticle which in many parts shows folds or wrinkles. At the lower surface of the organ of fixation there is a region in which the cuticle is pierced by numerous holes, the sieve plate. Through the latter a number of protoplasmatic excrescences are seen to protrude into the ovary. These excrescences form the proximal part of the root system; the more distal part of the latter is not distinctly visible in the sections of this specimen. At the sides of the parasite there are a few irregular layers of chitinous matter of a pronouncedly yellow colour. Probably these were formed by the host as a reaction against

the parasite. In the sections the ovary does not appear to be degenerated, though the eggs have remained comparatively small.

A section of the lower part of the organ of fixation of the same specimen is shown in Fig. 9*b* (p. 299). The cuticle of the organ of fixation in many parts is rather strongly wrinkled. The sieve plate is more or less convex, and contains a great number of openings. Irregular protoplasmatic excrescences are protruding through the sieve plate; in some parts these excrescences themselves are covered with a cuticle.

(2) Specimen on *E. vallentini* from St. WS 770 (Pl. XXXIX). The section gives a distinct view of the various parts of the parasite. The organ of fixation is more or less panduriform, as its ovoid internal part is connected by a rather narrow neck to the again broadening external part. From the latter the basal parts of a number of trophomeres take their origin. The section shows several groups of gonomeres

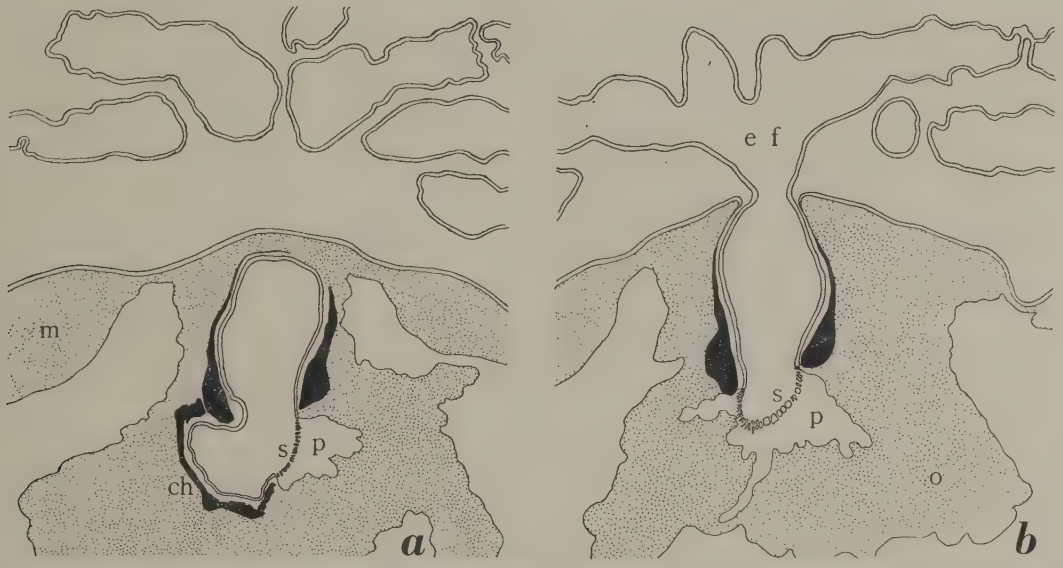

Fig. 2. *Amallocystis fagei* Boschma on *Euphausia vallentini* Stebbing from St. 892. Transverse sections of host, *a* from a more anterior region than *b*. Letters as in Fig. 1. ×80.

spreading in all directions. At the underside of the organ of fixation the sieve plate is visible; through this plate some protoplasmatic excrescences often of considerable length are seen to protrude into the ovary of the host. In this specimen again the ovary shows no obvious signs of degeneration. The developing eggs seem to be of normal appearance.

(3) Specimen on *E. vallentini* from St. 892 (Fig. 2). The chief details of two sections, separated by a distance of 40μ, are given in the figure. One section (*b*) shows the rather narrow neck connecting the internal and the external parts of the organ of fixation. The external part at its top divides into trophomeres which extend in various directions. The lower part of the organ of fixation shows a large sieve plate through which protoplasmatic excrescences are seen to protrude into the ovary of the host. At its sides the internal part of the organ of fixation is surrounded by masses of chitin. The other section (*a*) is from a slightly more anterior part of the host. Here the sieve plate is still visible, on one side of the parasite.

(4) Specimen on *E. frigida* from St. 766 (Fig. 3*a*). Here again there is a distinct constriction between the external and the internal parts of the organ of fixation. The cuticle of the internal part is rather strongly wrinkled, and the sieve plate is found on one side of the parasite. Sections of two trophomeres and of one gonomere are to be seen.

(5) Specimen on *E. frigida* from St. 665 (Fig. 3*b*). In this specimen the organ of fixation does not show a constriction between the external and the internal parts. The sieve plate is present on one side of the parasite. As in the preceding specimen the organ of fixation is largely surrounded by chitinous matter.

(6) Specimens on *E. vallentini* from St. WS 770 (Pl. XL). Here the Euphausiid is infested by two specimens of the parasite of approximately the same size and shape. One (the right of the upper figure of Pl. III) is embedded in the ovary of the host slightly before the other. The parasites show a distinct neck-like constriction between their external and internal parts. The figure shows the sieve plate of the hindmost of the two parasites, and the protoplasmatic excrescences protruding through this plate. In the upper part of the figure sections of a number of trophomeres and gonomeres are visible.

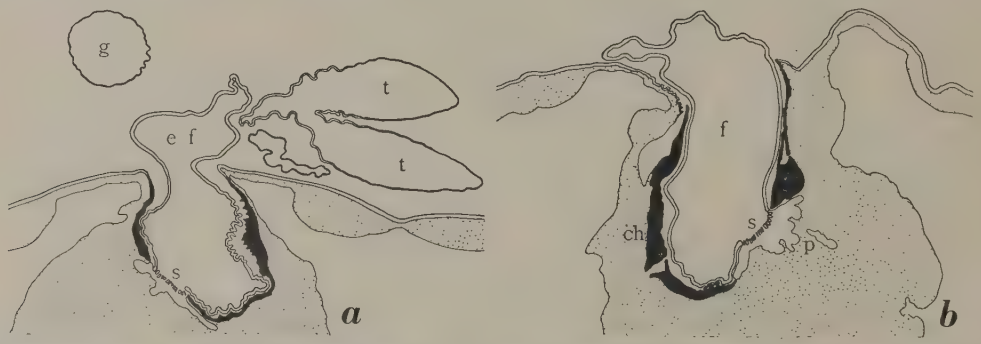

Fig. 3. *Amallocystis fagei* Boschma on *Euphausia frigida* H. J. Hansen. Transverse sections of hosts. *a*, specimen from St. 766; *b*, specimen from St. 665. Letters as in Fig. 1. In addition: *g*, gonomere. ×70.

A more enlarged photograph of part of a section next to the one of the upper figure is given in the lower figure of Pl. XL. It shows the lower part of the organ of fixation with the sieve plate and the protoplasmatic excrescences protruding through this plate. The figure shows further that the cuticle of the organ of fixation is rather thick, and that in some parts, especially in the right side of the figure, it is strongly wrinkled. On the proximal parts of the protoplasmatic excrescences also a cuticle has developed, though it is much thinner than that of the organ of fixation.

(7) Specimen on *E. frigida* from St. 751 (Fig. 4). The host was sectioned longitudinally. One of the sections (*a*) shows a median section of the parasite. Its organ of fixation does not present a pronounced constriction between the internal and external parts. The external part broadens into the common basal part of the trophomeres. The sieve plate is found in the lower part of the organ of fixation, pointing to the posterior region of the host. Through this plate protoplasmatic excrescences are seen to extend into the ovary of the host, where they divide into a well-developed root system. In this specimen the root system is pronouncedly different from other spaces in the ovary, so that the exact number of roots occurring in the sections could be drawn. At its sides the parasite is surrounded by irregular masses of chitin.

The other drawing (*b*) is after a section not far from the first one. It shows that the roots penetrate for a rather long distance towards the posterior region of the ovary of the host.

(8) Specimen on *Thysanoessa gregaria* from St. 871 (Fig. 5). Five sections are drawn, each section being at a distance of 20μ from the next. In the section of the most anterior part of the host (*a*) the cuticle of the organ of fixation is represented; on its inner wall it shows small excrescences which prove that this part represents the sieve plate. The next figure (*b*) shows the organ of fixation, a protoplasmatic excrescence, and some chitinous matter enveloping the organ of fixation. The next figure (*c*) does not

show any important changes. In the following figure (*d*) the organ of fixation is divided into a larger part which is largely external, and a smaller part in the lower region of the ovary of the host. In the last figure (*e*) this smaller part is still visible. It forms a distinct prolongation of the organ of fixation, penetrating the ovary of the host in a posterior direction. Moreover, the figures show sections of trophomeres and gonomeres above the dorsal surface of the host.

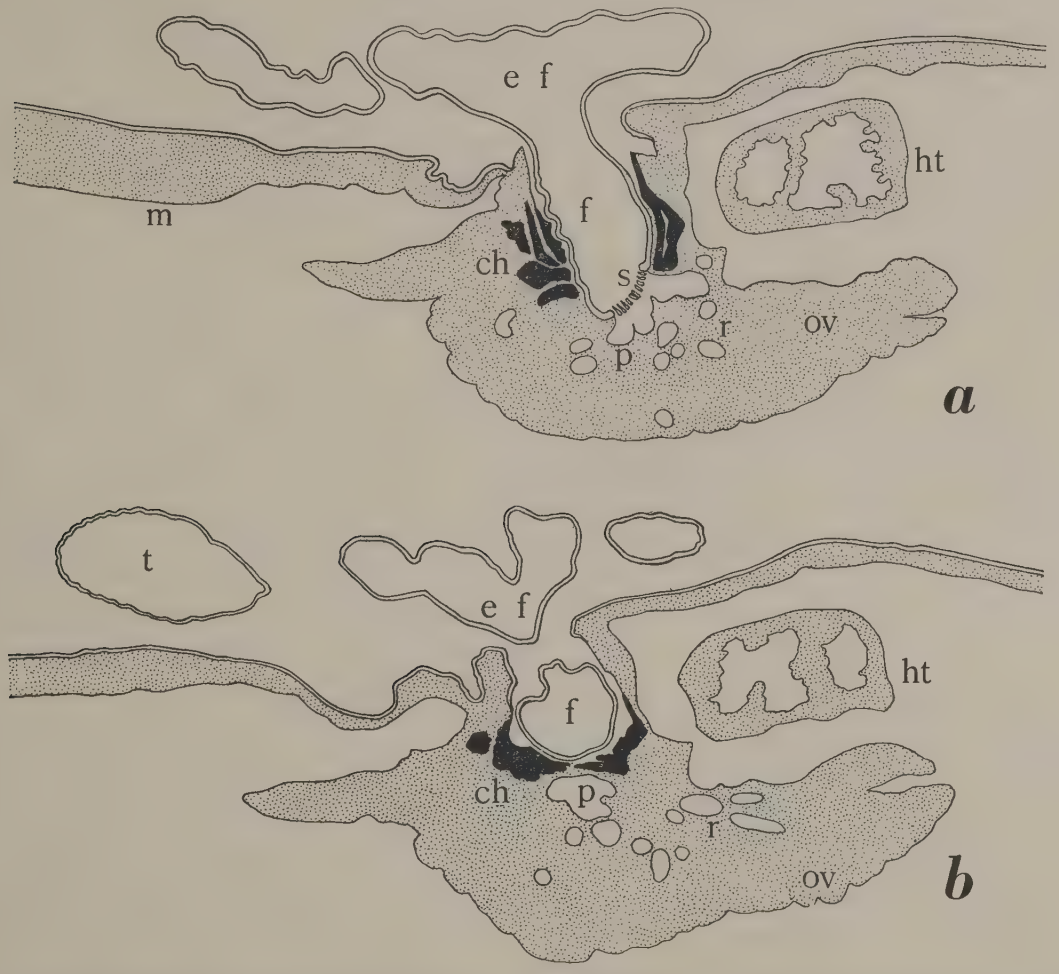

Fig. 4. *Amallocystis fagei* Boschma on *Euphausia frigida* H. J. Hansen from St. 751. Longitudinal sections of host; *a*, approximately in the median plane; *b*, slightly to one side. Letters as in Fig. 1. In addition: *ht*, heart of host; *ov*, ovary of host; *r*, roots. × 107.

It is interesting that the specimen on *Th. gregaria* is the only one in which the organ of fixation possesses a prolongation of the kind described here. In the other specimens examined the organ of fixation terminates in a blunt, somewhat broadened extremity.

Externally the parasites of the various species of Euphausiids are very much alike. The larger specimens may show a much larger number of trophomeres and gonomeres than the smaller specimens, and in the latter the size of the trophomeres and gonomeres may be smaller than in the former, but these differences do not point to a specific distinction. Moreover, internally the examined specimens are almost entirely similar. As the organ of fixation of the specimen on *Th. gregaria* possesses a distinct spur directed posteriorly, causing a slightly different aspect of this organ as compared to

that of the other specimens, this might point to a distinction. For the present, however, this difference seems to be of too little importance for a specific character, so that I am including the specimens on *Thysanoessa* in the species *Amallocystis fagei*.

On account of lack of sufficient material for comparison, and owing to deficient knowledge of the structure of the Euphausiacea, no attempt was made to determine the influence of the parasites on the sexual characters of the hosts. It may be observed here that all the parasitized specimens of which

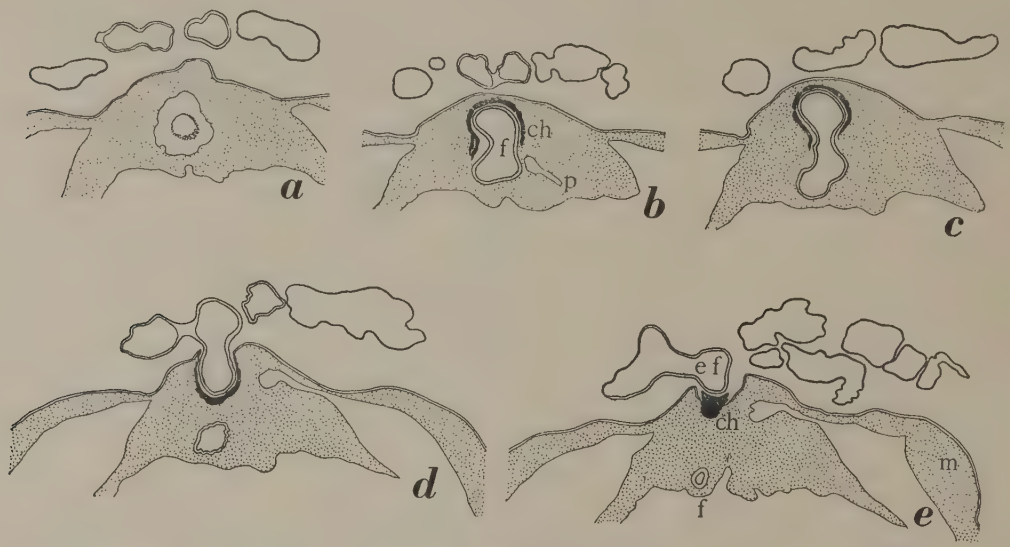

Fig. 5. *Amallocystis fagei* Boschma on *Thysanoessa gregaria* G. O. Sars from St. 871. Transverse sections of host. Letters as in Fig. 1. ×80.

sections were made are of the female sex. As already remarked above, the ovary of these infested specimens does not give the impression of being rudimentary or decidedly under-developed. It is quite possible, and it is even to be expected, that in normal specimens of the same size the ovary is much more fully developed. In Einarsson's infested specimens of *Thysanoessa inermis* and *Th. raschii* the ovary appeared to be completely disorganized, and these specimens did not show secondary sexual characters (cf. Einarsson, 1945). The differences in the state of development of the ovary in the specimens from the Antarctic as compared to Einarsson's specimens from the region of Iceland may be due to the fact that in the latter as a rule more than one parasite was found on each infested specimen, whilst in the former the parasite very rarely occurs in more than one specimen on one host.

Amallocystis umbellatus n.sp.

Material:

St. 81 (32° 45′ S, 8° 47′ W), 18. iv. 1926, net 450 H, depth of net 650–0 m., 1 ex. on *Hoplophorus novae-zeelandiae* De Man (Fig. 11).

St. 692 (02° 02′ 15″ N, 30° 08′ W), 9. v. 1931, net TYFB, depth of net 350–0 m., 1 ex. on *H. grimaldii* Coutière. Type specimen (Pl. XLI, figs. 1, 2, and Figs. 6–9*a*, 10). Transverse sections of part of host containing parasite, Delafield's haematoxylin.

Specific characters. External part consisting of numerous tufts of trophomeres and gonomeres, united with long stalks to the organ of fixation. Parasites of species of *Hoplophorus*, attached to the ventral surface of the first or second abdominal segment.

Of the two specimens the larger (the type specimen) was studied in sections, and of the other some particulars of its external part are mentioned below.

A. THE SPECIMEN ON *HOPLOPHORUS GRIMALDII* COUTIÈRE

The parasite (Pl. XLI, fig. 1) is attached to the ventral surface of the first abdominal segment of its host. Its external part consists of a large number of trophomeres with gonomeres which are arranged in separate tufts each provided with a stalk of considerable length. The tufts as a rule are composed of ten to twenty trophomeres (Fig. 6); in Pl. XLI, fig. 2, a side view of the whole mass of the external part, about fifteen of the tufts are visible. Assuming that approximately one-fifth of the total mass of tufts is visible in the figure the full amount of trophomeres in this specimen is estimated at 750–1500. The whole mass of trophomeres and gonomeres as shown in the figures in Pl. XLI has a greater diameter of 8 mm. and a height of 5 mm. The trophomeres have a conical shape, and they gradually broaden towards their distal extremity, where they bear two or three (as a rule three) gonomeres. The latter have a globular shape with the exception of the most distal gonomere, which as a rule is more or less elongated. The thickness of the gonomeres varies from 165 to 225 μ; the trophomeres are slightly thinner.

The arrangement of the trophomeres in tufts which are separately connected with long stalks to the organ of fixation gives the parasite a superficial resemblance to a compound umbel. This peculiarity is expressed in the trivial name *umbellatus*.

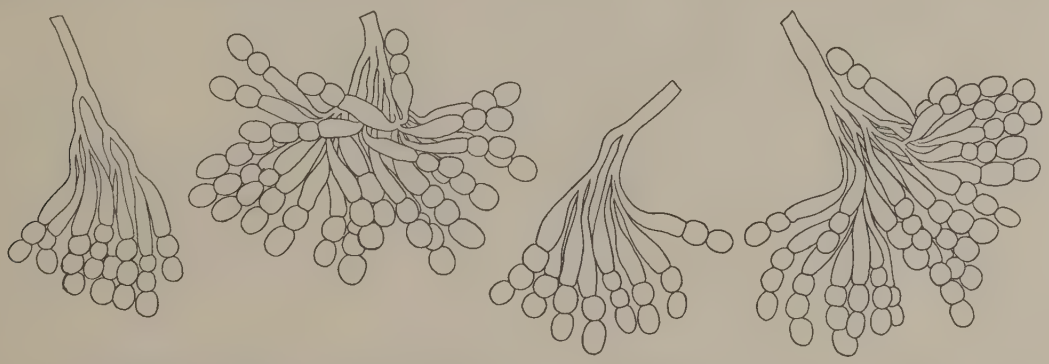

Fig. 6. *Amallocystis umbellatus* n.sp., type specimen. Tufts of stalks with trophomeres and gonomeres. × 15.

One section of the parasite with its external mass of tufts of trophomeres and gonomeres is represented in Fig. 7. In the region of this section the external part as well as the internal part of the organ of fixation are visible, the two parts being connected by a rather narrow neck. The internal part of the organ of fixation is surrounded by a number of roots, some of which penetrate into the marginal parts of the ventral nerve cord, whilst also in the tissues of the host directly under the cuticle there are also numerous roots. Some of these roots are found at a considerable distance from the organ of fixation, as, for instance, the one in the body musculature at the upper part of the left side of the figure.

The figure, moreover, shows sections of seven or eight tufts of trophomeres and gonomeres. Of some of these the stalks only are to be seen, of others stalks and trophomeres, and of others again trophomeres and gonomeres.

More details of the organ of fixation and of the root system are shown in Fig. 8. Here the stalks with their trophomeres and gonomeres are not represented in the figures. The parts belonging to the host are stippled, the organ of fixation with its rather strong cuticle is drawn with a double line, and the roots are drawn with single rather thick lines. Fig. 8*a* is the most anterior of the sections represented here; each following drawing is of a section from a more posterior region. The distances between the sections figured are: *a–b*, 100 μ; *b–c*, 110 μ; *c–d*, 90 μ; *d–e*, 140 μ; *e–f*, 120 μ; *f–g*, 90 μ; *g–h*, 100 μ; *h–i*, 80 μ; *i–j*, 140 μ. The section drawn in Fig. 7 is exactly between those of Fig. 8 *g* and *h*.

In Fig. 8*a* the anterior part (anterior in so far as it points to the anterior region of the host) of the organ of fixation is found in the peripheral part of the ventral nerve cord of the host. It is indicated

by *f*, and drawn with a double line, showing the thickness of its wall. In the peripheral part of the ventral nerve cord there are, moreover, four roots of the parasite. Six other roots are found in the body musculature of the host.

Fig. 8*b* does not differ in any important detail from Fig. 8*a*. The ventral nerve cord contains, besides the anterior part of the organ of fixation, four roots. Numerous roots are present in the body musculature of the host.

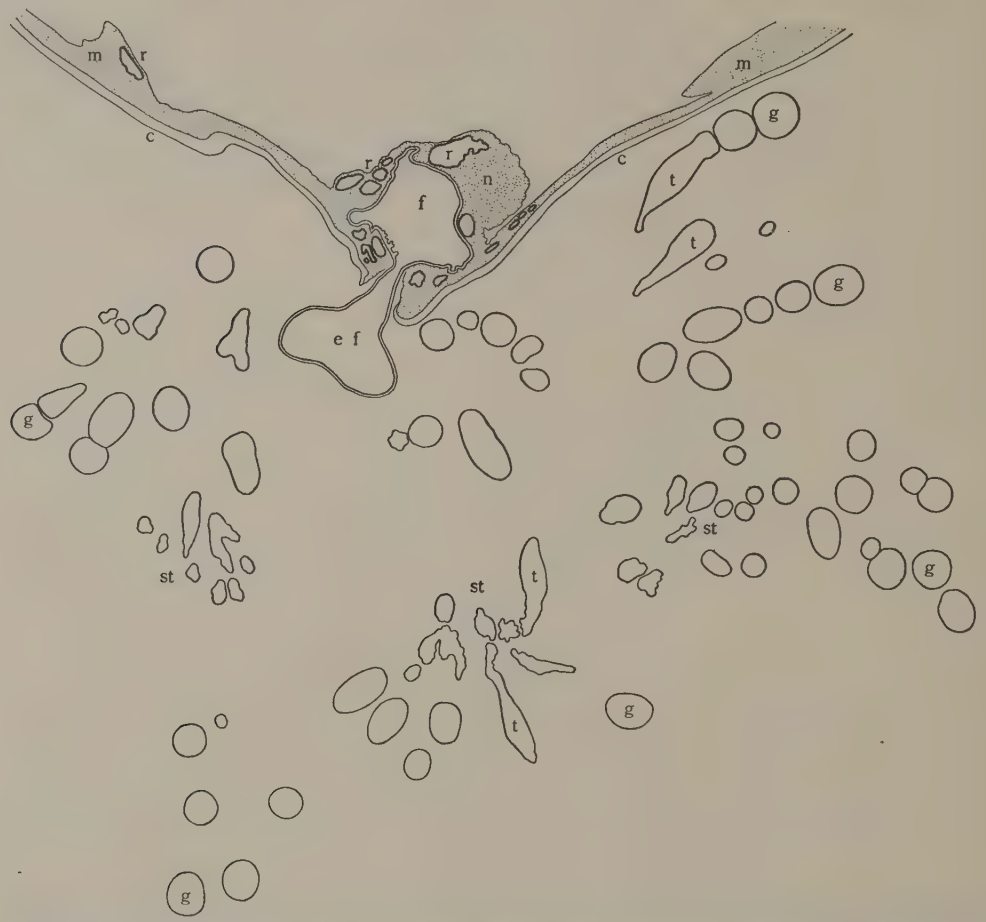

Fig. 7. Transverse section of the central part of the ventral region of the first abdominal segment of *Hoplophorus grimaldii* Coutière, with *Amallocystis umbellatus* n.sp., type specimen. Section from the region between those of Fig. 8 *g* and *h*. *c*, cuticle of host; *e f*, external part of organ of fixation; *f*, organ of fixation; *g*, gonomere; *m*, musculature of host; *n*, ventral nerve cord of host; *r*, root; *st*, stalks; *t*, trophomere. ×34.

In the section of Fig. 8*c* the organ of fixation is much wider. There are a few roots in the ventral nerve cord, some in or against the musculature under the cuticle, and some against another muscle (in the right side of the figure).

In Fig. 8*d* the ventral nerve cord is connected by a strand of tissue to the musculature covering the body wall. The parts of the parasite are not very different from those shown in Fig. 8*c*. One of the roots, in the peripheral region of the ventral nerve cord, is sectioned more or less longitudinally.

In the section shown in Fig. 8*e* the ventral nerve cord is connected to the body wall by a broad mass of tissue. The organ of fixation of the parasite here is already comparatively wide. There are a few roots of large size and a great number of smaller roots.

In Fig. 8*f* the organ of fixation forms a kind of neck protruding towards the body wall of the host. The ventral nerve cord is connected to the body of the host by means of a broad mass of tissue. Several large roots are visible here (one in the musculature at some distance from the median plane, at the left side of the figure), and numerous smaller roots.

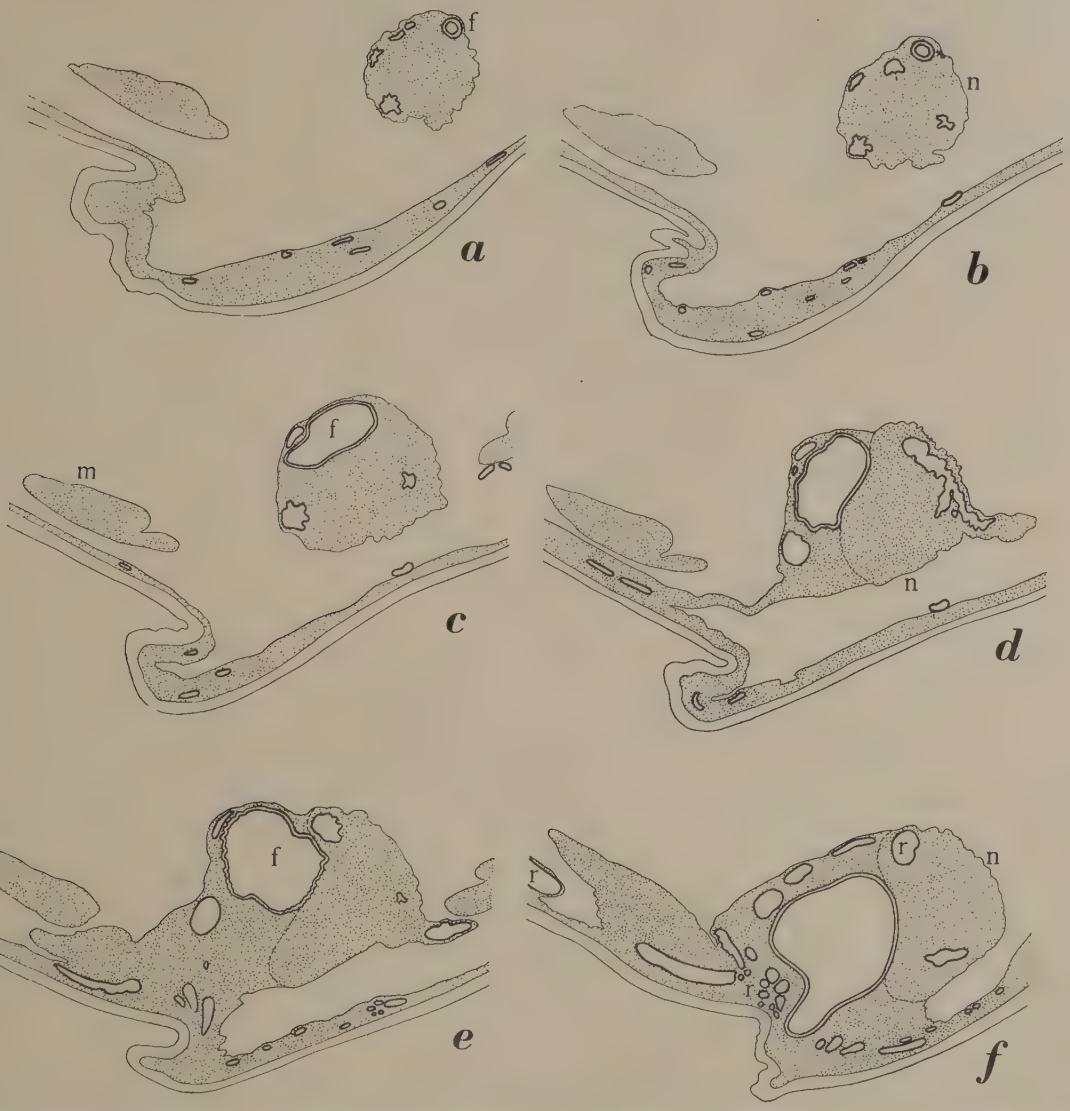

Fig. 8*a–f*. Transverse sections of the central part of the ventral region of the first abdominal segment of *Hoplophorus grimaldii* Coutière, with *Amallocystis umbellatus* n.sp., type specimen. *a* from a slightly more anterior region than *b*, each following section from a more posterior region. Stalks, trophomeres and gonomeres omitted. Letters as in Fig. 7. ×45.

Fig. 8*g* shows the organ of fixation in the region in which it attains its largest size. Its middle part is more or less constricted and forms a kind of neck uniting the internal part to the external part. Surrounding the internal part of the organ of fixation there are a great many large and smaller roots. One of these roots has a rather thick wall. It is the proximal part of one of the larger roots.

In Fig. 8*h* the external part of the organ of fixation is visible as a triangular mass next to the body wall of the host. The internal part of the organ of fixation and a great number of roots of various sizes are to be seen in the mass of tissue connecting the ventral nerve cord to the body wall, and in the

ventral nerve cord itself. A few of the roots which have just branched off from the organ of fixation have a rather strong wall, drawn with a double line in the figure. The internal part of the organ of fixation in this section shows the proximal parts of some large roots (in the upper and in the lower parts). Moreover, in the organ of fixation there is a series of cuticular formations which undoubtedly represent a sieve plate. In the section there is a series of small cuticular bars arranged in a crescentic row. Inside and outside this row there are a few more of these cuticular formations, so that the sieve plate is not as distinct as in *Amallocystis fagei*. More details of this sieve plate will be noted below.

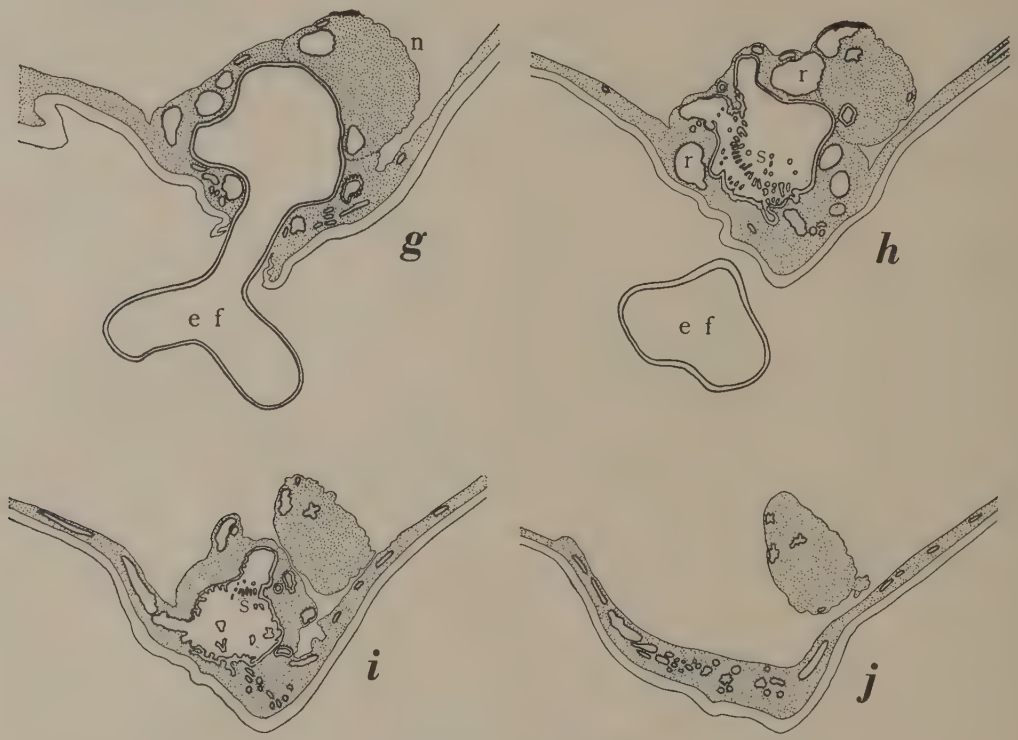

Fig. 8 *g–j*. For explanation see Fig. 8*a–f*. In addition: *s*, sieve plate. ×45.

In the section of Fig. 8*i* the ventral nerve cord is no longer connected with the mass of tissue enveloping the parasite. In the nerve cord itself there are still a few roots. The internal part of the organ of fixation shows one root penetrating into the musculature of the body wall (in the left half of the figure). Moreover, there is one large root in the upper part of the organ of fixation. This root is partially separated from the organ of fixation by a sufficiently distinct sieve plate. On the wall of the organ of fixation there are numerous more or less irregular cuticular excrescences, and in the interior of this organ there are a few irregular masses of cuticular matter, the whole forming a part of, or being connected with, the sieve plate of the section in Fig. 8*h*.

The last section represented here (Fig. 8*j*) shows parts of the root system, in the ventral nerve cord as well as in the musculature of the body wall. Especially in the latter there are a great number of roots.

The internal part of the organ of fixation, as it appears in the section preceding that in Fig. 8*h*, is drawn on a larger scale in Fig. 9*a*. The organ of fixation is covered with a comparatively thick cuticle, which is also present on the thick roots extending from the organ of fixation. In the lower part of the figure there are more or less irregular excrescences of the cuticle which protrude as a trabecular mass into the organ of fixation. This trabecular mass is arranged in a more or less crescentic manner,

partially dividing the left part of the organ of fixation from the larger right part. Now from this left part the large roots take their origin (cf. also Fig. 7*h*), and the whole configuration of this part of the organ of fixation presents a striking similarity to that found in *A. fagei* (cf. Fig. 9*b*).

In *A. fagei* the organ of fixation has a rather thick cuticle (necessary to ensure a solid fixation of the parasite in its host); part of this cuticle is pierced by a system of holes so that a sieve plate is formed through which protoplasmatic excrescences (the roots) can protrude. In *A. fagei* the proximal parts of these roots may also develop a cuticle, as in the specimen of Fig. 9*b*.

The external part of *A. fagei* does not show more than about fifty trophomeres, so that the parasite is securely fixed to its host by means of the simple globular or oval organ of fixation. In *A. umbellatus*, however, which may have 750–1500 trophomeres, this enormous mass of external organs necessitates the strengthening of the organ of fixation into an immovable organ of anchorage. Originally in the specimen of *A. umbellatus* described here the organ of fixation may have had a shape quite similar to

Fig. 9*a*. *Amallocystis umbellatus* n.sp., type specimen. Section preceding the one of Fig. 8*h*. Organ of fixation with sieve plate. *f*, organ of fixation; *r*, root. × 163.

Fig. 9*b*. *Amallocystis fagei* Boschma, type specimen. Section of lower part of organ of fixation. *f*, organ of fixation; *p*, protoplasmatic excrescences; *s*, sieve plate. × 283.

that found in *A. fagei*. It must have had a strong cuticle, but the part of the organ of fixation to the left of the sieve plate in Fig. 9*a* probably had a thin cuticle, so that the protoplasmatic excrescences (the roots) might absorb food from the host. Gradually the root system became more divided and more strongly developed; at the same time the number of external parts (trophomeres and gonomeres) increased, necessitating a stronger fixation of the parasite. The proximal parts of the root system now became covered with a thick and strong cuticle, thereby forming a part of the organ of fixation in securing a stronger hold of the parasite on its host. The sieve plate which was present between the organ of fixation and the roots now had lost its direct function, but it remained as it was, and the process of formation of a trabecular mass of cuticular excrescences even continued, so that now in some parts two rows of trabeculae are visible.

In the type specimen of *A. umbellatus* the sieve plate therefore appears to be an organ which has had its use as long as the parasite was comparatively young and possessed a few trophomeres only. It has lost its real function now, but it has remained where it originally developed. A comparison with the sieve plate of *A. fagei* shows that the trabecular mass in *A. umbellatus* must be regarded as being homologous with the former.

The internal part of the organ of fixation forms a more or less bulbous expansion which is protracted

into a long pointed spur extending in the anterior direction of the host. In this respect the organ of fixation of *A. umbellatus* corresponds exactly with that of *A. fasciatus*, in which Fage (1936) described a similar excrescence. Moreover, in *A. fasciatus* the organ of fixation has a number of shorter excrescences of varying shape pointing in a lateral or posterior direction (Fage, 1936, fig. ii*c*). In all probability the latter represent the proximal part of the root system, as they show a certain similarity to the corresponding parts of *A. umbellatus*, where the large proximal roots are confined to the region of the parasite turned towards the posterior part of the host.

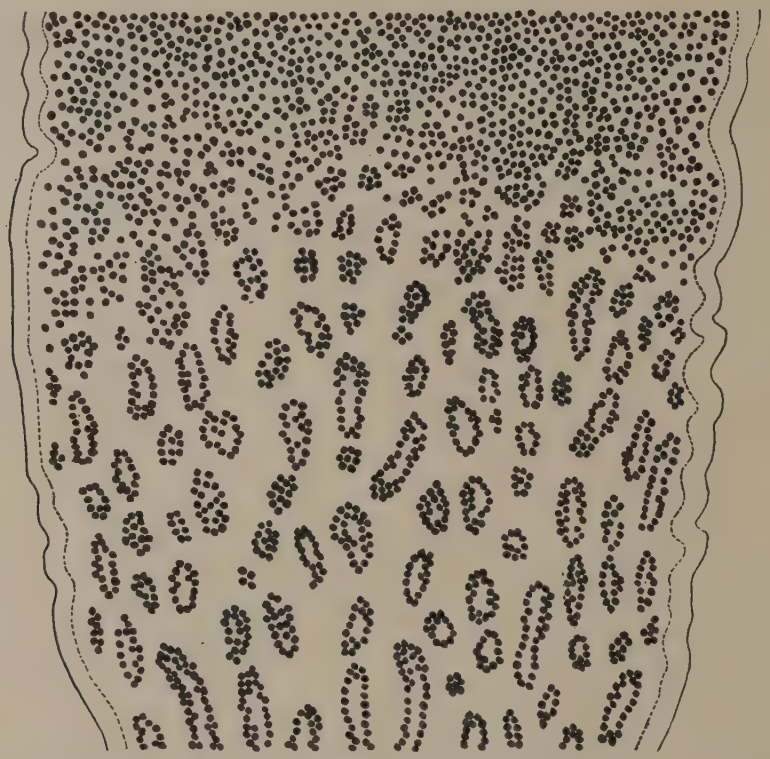

Fig. 10. *Amallocystis umbellatus* n.sp., type specimen. Part of a longitudinal section of a trophomere, showing the arrangement of the nuclei. ×825.

No studies were made of cytological details of the parasite. A few remarks on the trophomeres and the gonomeres may be given here. In the stained sections the trophomeres have a pink colour, the younger gonomeres may have the same colour or may have become a slightly darker red. The older gonomeres are stained much more deeply, and often show a dark blue colour. In the gonomeres the nuclei appear to be more or less evenly distributed throughout the whole organ. In the trophomeres, however, there is a distinct difference between the proximal part and the distal region. In the proximal part the nuclei are arranged in groups so as to form clusters that with their greater diameter are more or less parallel to the longitudinal axis of the trophomere. This occurs in about the whole of the proximal third part of the trophomere. In a more distal region the groups of nuclei become more indistinct, and finally the nuclei become more or less evenly distributed in the trophomere. The region of transition of the groups of nuclei into a rather uniformly scattered mass of nuclei is shown for one of the trophomeres in Fig. 10. It appears as if in the proximal region of the trophomeres the nuclei are found on more or less parallel strands of tissue, whilst they do not occur in the intervening spaces. The phenomenon referred to here is to be observed in all the trophomeres of the series of sections.

B. THE SPECIMEN ON *HOPLOPHORUS NOVAE-ZEELANDIAE* DE MAN

The specimen is attached to the ventral surface of the abdomen of its host, and the external part protrudes through the integument joining the first and second abdominal segments. The parasite was examined externally only, but the pleurae of the left first and second abdominal segments were removed to obtain a better view of the parasite. In the side view of the external parts of the parasite (Fig. 11*b*) the pleurae are represented to show the situation of the parasite in regard to its host. In the figure approximately 100 trophomeres with their gonomeres are visible. If we assume that about one-fifth of the whole number of trophomeres is visible here, the total number amounts to 500, a considerably smaller number than that of the type specimen. As in the latter the trophomeres are united in tufts that with usually long stalks originate from a common centre. The whole external mass in side view has a larger diameter of about 5 mm., and a height of about 2 mm.

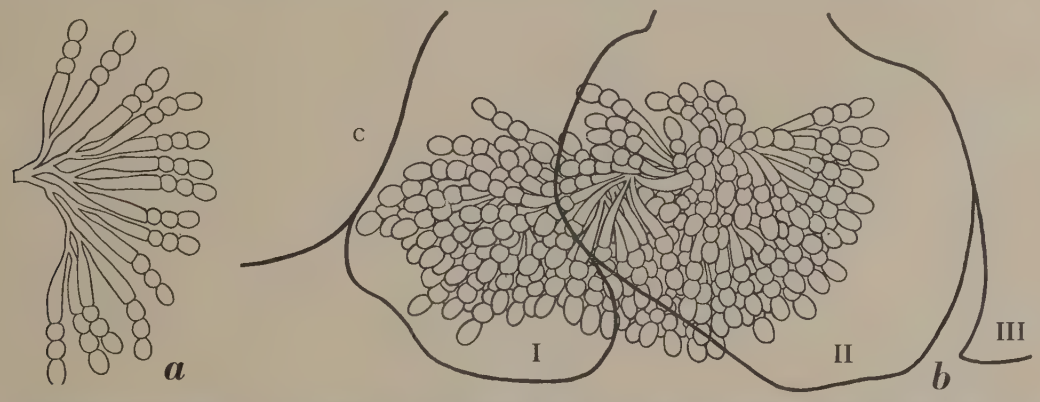

Fig. 11. *Amallocystis umbellatus* n.sp., specimen on *Hoplophorus novae-zeelandiae* De Man. *a*, tuft of stalks with trophomeres and gonomeres; *b*, external part of parasite *in situ* on host. *c*, carapace; I, first abdominal segment; II, second abdominal segment; III, third abdominal segment. × 15.

Fig. 11*a* represents a single tuft of trophomeres and gonomeres. As a rule each trophomere bears three gonomeres, which are of a globular shape except the distal gonomere which is usually slightly more elongated. The diameter of the gonomeres varies from 140 to 195 μ. They are, therefore, slightly smaller than those of the specimen on *Hoplophorus grimaldii*, but in all other respects the external part of the two parasites is quite similar.

The host of the type of *Amallocystis umbellatus*, a specimen of *Hoplophorus grimaldii* Coutière, appears to be a female. The pleopods of the first and second abdominal segments seem to be of normal shape. Every trace of an appendix masculina as it occurs on the second pleopod of the male is absent. Moreover, the anterior angle of the first abdominal pleuron is evenly rounded, without any indication of an incision, so that this pleuron has the typical character of the female.[1]

The host of the other specimen of *Amallocystis umbellatus*, *Hoplophorus novae-zeelandiae* De Man, again has all the characters indicating the female sex. Here also the pleopods of the first and second abdominal segments show a normal development, whilst the appendix masculina is entirely absent. As in the former specimen there seem to be no indications of a deviation from the normal type as a result of the parasitization.

[1] Cf. Chace, Jr., F. A., 1940, Plankton of the Bermuda Oceanographic Expeditions. IX. The Bathypelagic Crustacea. *Zoologica*, vol. xxv, p. 188 (concerning *Hoplophorus grimaldii* Coutière): 'Although there is a well developed appendix masculina in the adult males of this species, there is also a sexual distinction involving the first abdominal pleuron as in the preceding species; in the male, the lower anterior angle of this pleuron is deeply incised so that the angle formed approaches a right angle, while in the female this angle, if present at all, is very obtuse.'

Amallocystis capillosus Fage

Amallocystis capillosus Fage, 1938, p. 287.

Material:

St. WS 748 (53° 41′ 30″ S, 70° 55′ 00″ W), 16. ix. 1931, net NR, depth of net 300 (0 - ?) m., 2 ex. on *Pasiphaea acutifrons* Bate (Pl. XLI, figs. 3, 4). One specimen, transverse sections of part of host containing parasite, Delafield's haematoxylin (Figs. 12–16).

The parasite is attached to the basal part of the rostrum of the host, where it forms a pronounced ridge on the carapace. The external part of one of the parasites is a mass of stalks with trophomeres and gonomeres with a larger diameter of about 4·6 mm. and a height of about 3·5 mm. (Pl. XLI, fig. 3); the corresponding dimensions of the external part of the other parasite (the sectioned specimen) are about 4 by 3·5 mm. (Pl. XLI, fig. 4). In the external masses of each of the two parasites about fifty to seventy trophomeres can be counted, though originally there must have been a considerably larger number, as in Fig. 15 already parts of eighty-three trophomeres are visible, the majority of these being sections of the stalks. Apparently a great number of trophomeres have become detached from their stalks after preservation of the parasites.

At each side of the carina which forms the proximal part of the rostrum of the host there is a bundle of slender stalks of various lengths, sometimes extending rather far in an anterior direction. At its extremity each stalk passes into a trophomere of an elongate shape, more or less cylindrical with a tapering proximal part. On the top of each trophomere there may occur one gonomere of elongatedly oval shape, which may have a length of about 0·6 mm., whilst the trophomere may be about twice as long. The transverse diameter of the trophomeres and the gonomeres is from 0·15 to 0·25 mm.

The internal part of the parasite was studied in transverse sections of the rostral region of the host. Drawings of three sections containing the internal part of the parasite are given here. The most anterior (Fig. 12) is at a distance of 60μ from the following (Fig. 13), the latter at a distance of 170μ from the next figured section (Fig. 14). Moreover, part of a section not containing internal parts of the parasite is drawn in Fig. 15. This section is at a distance of 330μ from the one drawn in Fig. 12.

The series of sections begins at the posterior region of the part of the host sectioned, so that the right side of the host is found at the left side of the figures.

In Fig. 12 at each side of the carina (the proximal part of the rostrum) there is a number of stalks, of trophomeres and gonomeres. Some of the stalks are drawn with a double line, as they have a rather thick cuticle; they belong to the proximal portions of the external part of the parasite. At the right side of the basal part of the carina (left in the figure) the latter is pierced by a hole through which the external part of the organ of fixation of the parasite protrudes. This external part here forms a short tube which at its top divides into a number of stalks. Between the carina and the antennal gland of the host (indicated by a broken line) there is an irregular mass of cuticular matter belonging to the parasite; this mass represents the proximal part of the root system. The figure further shows a number of roots extending into the tissues of the host (the roots indicated with a rather heavy line).

Fig. 13 shows again at each side of the carina a number of stalks, of trophomeres and of gonomeres of the parasite. The organ of fixation in the region of this section attains its largest size. It is a more or less irregularly globular organ, which in the figured section forms an excrescence penetrating through a hole at the left side of the basal region of the carina (right in the figure). This excrescence is of a similar shape to the one in Fig. 12; at its top it divides into a number of stalks. The organ of fixation itself is covered with a rather thick wall, which in its lower part shows a peculiar structure that must be considered to be homologous with the sieve plate as it occurs in *Amallocystis fagei*. Under this sieve plate there is a dense mass of cuticular matter with a great number of openings; it is a complicated

canal system with strong cuticular walls, or a mass of trabecular cuticular bars leaving openings between themselves. In the figures this mass is indicated as the proximal part of the root system. From this proximal part of the root system a large branch extends to the left (to the right in the figure), and

Fig. 12. Transverse section of the rostral region of *Pasiphaea acutifrons* Bate with *Amallocystis capillosus* Fage. *e f*, external part of organ of fixation; *g*, gonomere; *gl*, antennal gland of host; *pr*, proximal part of root system; *r*, roots; *rs*, rostrum of host; *st*, stalks. ×67.

at its end this branch divides into smaller roots which in the section of the figure show their cuticular walls only. Another branch of the proximal root system is to be seen directly under the main mass. This branch consists of cuticular matter with very small openings. A third branch of the proximal root system is visible in the lower part of the figure. In this branch the openings are large in comparison to the cuticular matter. The figure further shows some roots with thin walls (though drawn with rather heavy lines) in the vicinity of the antennal gland, at each side of the median plane.

Fig. 14 shows again at each side of the carina sections of a number of stalks, of trophomeres and of gonomeres. Here there is a second hole at the right side of the basal region of the carina (left in the figure). Through this hole an excrescence of the organ of fixation protrudes, thereby becoming external. At its top it divides into a number of stalks. One side of the internal part of the organ of

Fig. 13. Same specimen as Fig. 12, a slightly more posterior section. Letters as in Fig. 12. In addition: *f*, organ of fixation; *s*, sieve plate. ×67.

fixation shows the connexion with the proximal part of the root system, the complicated mass of cuticular matter with numerous openings of various sizes. A few roots with thin walls are to be seen in the tissues surrounding the organ of fixation.

In the sectioned specimen therefore the organ of fixation possesses one excrescence which at the left side of the host pierces the basal part of the rostral carina, and two excrescences which at some distance from each other independently traverse the cuticle at the right side of the basal part of the rostral carina.

The sections in Figs. 12–14 show a comparatively small quantity of stalks and trophomeres and gonomeres; in a more anterior region of the host this number is considerably larger, as in the section after which Fig. 15 was drawn. At the left side of this figure not all the external parts of the parasite have been represented. The shrunken appearance of some of the trophomeres or gonomeres in all probability is a result of the preservation of the material.

Fig. 14. Same specimen as Figs. 12 and 13, a slightly more posterior section than the one of Fig. 13. Letters as in Fig. 12. In addition: *f*, organ of fixation. ×67.

The sieve plate of the sectioned specimen is shown on a larger scale in Fig. 16. Here *a* is a part of the section shown in Fig. 13, and *b* is a part of a section between those of Figs. 13 and 14, at a distance of 30*μ* from the section of Fig. 14. Each of the two figures shows a distinct sieve plate, as distinct as that found in *A. fagei*, but behind this sieve plate there is very little open space, as the part of the parasite referred to here as the proximal part of the root system almost immediately joins here the organ of fixation. This proximal part of the root system is a cuticular mass with comparatively irregular

openings, or, more precisely, it is an intricate mass of trabecular cuticular matter which leaves but little space between the bars and lamellae composing this cuticular mass. In Fig. 16*b* the connexion of the internal part of the organ of fixation with the root system through the sieve plate is more apparent than in Fig. 16*a*.

Undoubtedly young specimens of *A. capillosus* possess a sieve plate through which protoplasmatic excrescences from the internal part of the organ of fixation penetrate into the tissues of the host.

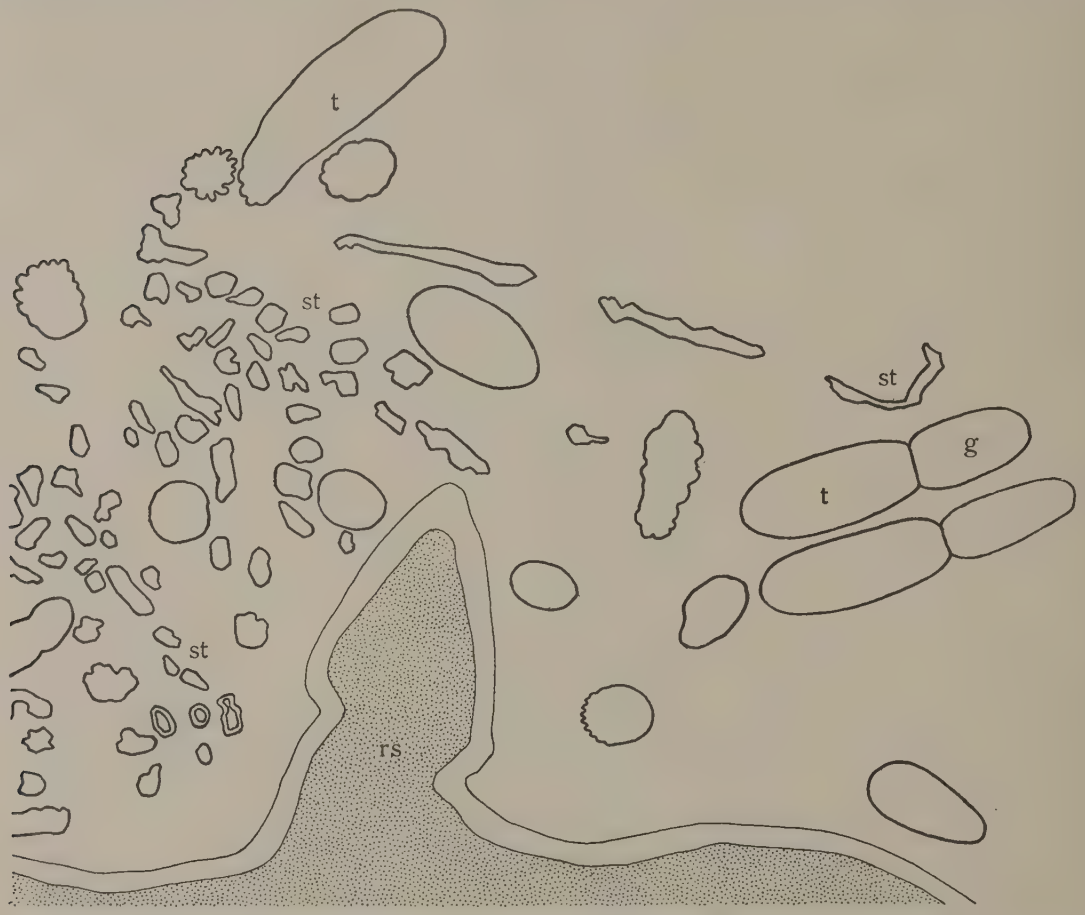

Fig. 15. Same specimen as Figs. 12–14, transverse section of the rostral region slightly behind the base of the free rostrum. Letters as in Fig. 12. In addition: *t*, trophomere. ×67.

During further development the increasing volume of the external part of the parasite causes a need for a stronger fixation of the internal parts. As the functioning root system then has penetrated for a comparatively long distance into the organs of the host, the proximal part of the root system then can be added to the organ of fixation by the formation of additional cuticular matter. The sieve plate, which in young stages must have formed an important part of the parasite, during growth of the organism gradually must have lost its original function. Though in older stages it is no more of special use to the parasite, the sieve plate has remained where at first it was formed.

Fage (1938) describes the lower surface of the organ of fixation of *A. capillosus* as having a rough surface. In the figure (loc. cit., fig. 3) this is also indicated. Undoubtedly the specimens examined by Fage had the same structure of the internal parts as the specimen described above. The rough

surface of the organ of fixation in Fage's specimens in reality was the proximal part of the root system with its intricate trabecular mass of cuticular matter, bringing about a pronouncedly uneven surface of this part of the parasite.

The six specimens of *Pasiphaea tarda* Kröyer from the Skagerrak infested with *Amallocystis capillosus* Fage were all of the male sex. Curiously enough the two specimens of *Pasiphaea acutifrons* Bate from the Strait of Magellan bearing the same parasite are both females. They do not show any indication of differences from normal females, as might be expected as a result of the parasitization. As, however, no material of uninfested specimens of this rare species was available, it is not altogether certain that in every respect they are of normal appearance.

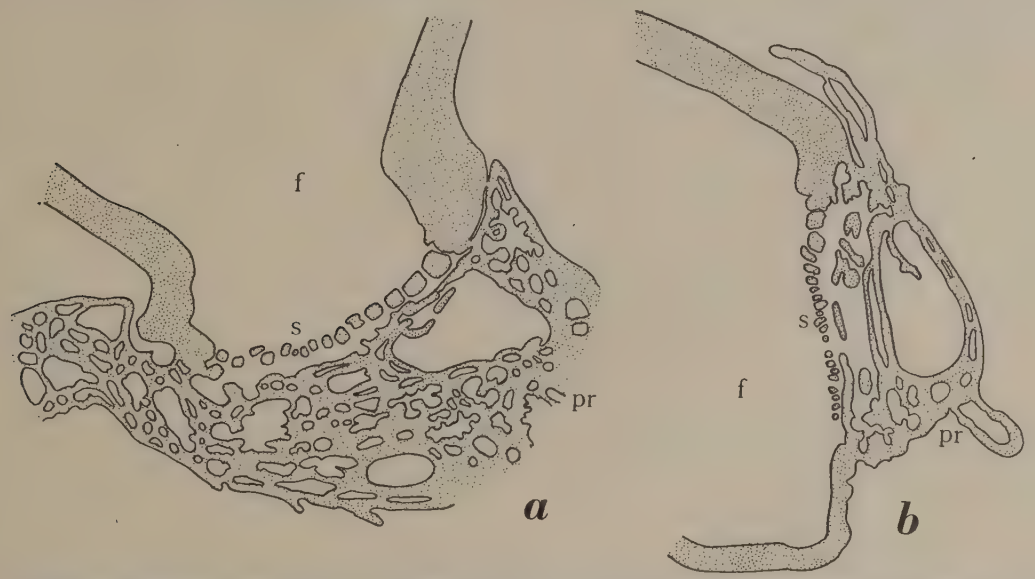

Fig. 16. *Amallocystis capillosus* Fage, specimen of Figs. 12–15. *a*, detail of fig. 13, further enlarged; *b*, sieve plate of section between those of Figs. 13 and 14. *f*, organ of fixation; *pr*, proximal root system; *s*, sieve plate. × 190.

THE CHARACTERS OF THE SPECIES OF THE GENUS *AMALLOCYSTIS*

A synopsis of the characters of the described forms of the genus *Amallocystis*, based on data from the literature and on those of the present paper, shows the following particulars.

(1) The parasite mentioned and figured by Bate (1888)

Host and manner of attachment: *Pasiphaea cristata* Bate, ventral surface of second abdominal segment.

Number and arrangement of trophomeres: Approximately fifty (?), in a bundle spreading from a common centre.

Shape of trophomeres and gonomeres: Trophomeres elongately cylindrical or conical, twice or $2\frac{1}{2}$ times as long as broad; gonomeres globular to oval.

Number of gonomeres on each trophomere: Three.

Dimension of gonomeres: Unknown.

Organ of fixation: Unknown.

(2) *Amallocystis racemosus* (Coutière)

Host and manner of attachment: *Pasiphaea tarda* Kröyer, ventral surface of third abdominal segment.

Number and arrangement of trophomeres: About fifty, in a single bundle attached to a common basal organ of fixation. Total length of the trophomeres with their gonomeres up to 4 mm.

Shape of trophomeres and gonomeres: Trophomeres elongately cylindrical, gonomeres oval, to about twice as long as broad.

Number of gonomeres on each trophomere. Up to seven.

Dimensions of gonomeres: Transverse diameter on an average $\frac{1}{2}$ mm. (Coutière, 1911*c*, text), 0·18–0·3 mm. (Coutière, 1911*c*, text-fig. i), 0·3–0·4 mm. (Coutière, 1911*c*, pl. viii, fig. 1).

Organ of fixation: A cylindrical hollow stalk terminating inside the host as a blunt cone.

(3) *Amallocystis fasciatus* Fage

Hosts and manner of attachment: *Gnathophausia zoea* Will.-S., ventral surface of first abdominal segment. Also on *Gnathophausia ingens* (Dohrn).

Number and arrangement of trophomeres: About 150, arranged in tufts of five or six, with short stalks attached to the external part of the organ of fixation. Total length of the trophomeres with their gonomeres 1·5 mm.

Shape of trophomeres and gonomeres: Trophomeres cylindrical, gonomeres oval, the latter twice as long as broad or slightly more elongated.

Number of gonomeres on each trophomere: As a rule one, rarely two or three.

Dimensions of gonomeres: Transverse diameter 0·2 mm.

Organ of fixation: Showing a number of excrescences terminating with blunt extremities into the tissues of the host; one excrescence much larger than the others, pointing in anterior direction of the host.

(4) *Amallocystis umbellatus* n.sp., type specimen

Host and manner of attachment: *Hoplophorus grimaldii* Coutière, ventral surface of first abdominal segment.

Number and arrangement of trophomeres: About 750–1500 trophomeres in tufts of ten to twenty, each tuft with a long slender stalk attached to external part of organ of fixation.

Shape of trophomeres and gonomeres: Trophomeres conical to cylindrical, gonomeres globular, the distal gonomere somewhat elongated.

Number of gonomeres on each trophomere: Two or three (as a rule three).

Dimensions of gonomeres: Transverse diameter 165–225μ.

Organ of fixation: External part broadened, dividing into the basal parts of the stalks. Internal part more or less globular, with one long pointed excrescence extending in anterior direction of host. External and internal parts of organ of fixation connected by a somewhat narrower neck. Between proximal part of root system and organ of fixation a sieve plate.

(5) *Amallocystis umbellatus* n.sp., second specimen

Host and manner of attachment: *Hoplophorus novae-zeelandiae* De Man, ventral surface of abdomen, in integument joining first and second segments.

Number and arrangement of trophomeres: About 500, in tufts of ten to twenty, each tuft with a long slender stalk attached to external part of organ of fixation.

Shape of trophomeres and gonomeres: Trophomeres conical to cylindrical, gonomeres globular, the distal gonomere somewhat elongated.

Number of gonomeres on each trophomere: Two or three (as a rule three).

Dimensions of gonomeres: Transverse diameter 140–195μ.

Organ of fixation: Not examined.

(6) *Amallocystis capillosus* Fage, type specimens

Host and manner of attachment: *Pasiphaea tarda* Kröyer, base of rostrum.

Number and arrangement of trophomeres: About fifty, in two bundles, at each side of the rostrum of the host one.

Shape of trophomeres and gonomeres: Trophomeres with long slender stalks, cylindrical or basal part conical, length 1–1·3 mm., diameter 0·25 mm. (Fage, 1938, text, 0·025 mm.; ibid., fig. 2, 0·25 mm.). Gonomeres cylindrical.

Number of gonomeres on each trophomere: Not more than one.

Dimensions of gonomeres: Transverse diameter 0·25 mm. Length twice the breadth or more.

Organ of fixation: A hyaline plate with rough surface, in transverse position under the rostrum, extending at each side into an excrescence penetrating through the cuticle of the host.

(7) *Amallocystis capillosus* Fage, specimens from the Discovery collections

Host and manner of attachment: *Pasiphaea acutifrons* Bate, base of rostrum.

Number and arrangement of trophomeres: About fifty to seventy (originally probably more), arranged in two tufts each to one side of the rostrum.

Shape of trophomeres and gonomeres: Trophomeres more or less cylindrical with a proximal part tapering into the long slender stalk; gonomeres elongately oval. Trophomeres about twice as long as gonomeres.

Number of gonomeres on each trophomere: Not more than one.

Dimensions of gonomeres: Length about 0·6 mm., transverse diameter from 0·15 to 0·25 mm.

Organ of fixation: Irregularly globular, in its upper part with excrescences penetrating through the cuticle of the host, in its lower part possessing a sieve plate forming the connexion of the organ of fixation with the proximal part of the root system.

(8) *Amallocystis* sp., Einarsson (*Amallocystis fagei* Boschma)

Hosts and manner of attachment: *Thysanoessa inermis* (Kröyer) and *Th. raschii* (M. Sars), dorsal surface of the carapace in the region of the genital gland or (exceptionally) in the region of the stomach. As a rule more than one parasite on each host.

Number and arrangement of trophomeres: Numerous trophomeres (about thirty ?) spreading from the external part of the organ of fixation.

Shape of trophomeres and gonomeres: Trophomeres conical to cylindrical, gonomeres globular to oval.

Number of gonomeres on each trophomere: Up to nine (from one to ten constrictions in the sausage-like elongations, Einarsson, loc. cit.).

Dimensions of gonomeres: Transverse diameter approximately 100μ (measured in fig. 83 of Einarsson, loc. cit.).

Organ of fixation: Consisting of an internal irregularly oval part and an external part divided into the basal extremities of the trophomeres, the two parts connected by a rather narrow neck.

(9) *Amallocystis fagei* Boschma, specimens from the Discovery collections

Hosts and manner of attachment: *Euphausia vallentini* Stebbing, *E. frigida* H. J. Hansen, *E. recurva* H. J. Hansen, *E. lucens* H. J. Hansen, *E. hemigibba* H. J. Hansen, *Thysanoessa gregaria* G. O. Sars. Dorsal surface of carapace in the region of the genital gland.

Number and arrangement of trophomeres: Parasites of *Euphausia vallentini* and *E. frigida*, thirty to fifty; parasites of *E. recurva*, *E. lucens*, *E. hemigibba* and *Thysanoessa gregaria*, ten to fifteen. In a single tuft spreading from the external part of the organ of fixation.

Shape of trophomeres and gonomeres: Trophomeres conical to cylindrical, gonomeres more or less globular, the distal gonomere often somewhat elongated.

Number of gonomeres on each trophomere: Up to seven.

Dimensions of gonomeres: Parasites of *Euphausia vallentini* and *E. frigida*, transverse diameter 0·16–0·33 mm.; parasites of *E. hemigibba*, *E. recurva* and *Thysanoessa gregaria*, transverse diameter 0·13–0·16 mm.

Organ of fixation: External part broadened, dividing into the basal parts of the stalks, internal part globular or oval; the two parts united by a neck which, as a rule, is rather narrow. In a specimen on *Th. gregaria* the internal part of the organ of fixation has a pointed excrescence directed towards the posterior region of the host. Sieve plate in the lower part of the organ of fixation.

The data compiled above show that the species of *Amallocystis* can easily be characterized by means of their external parts only. These characters are the following.

Amallocystis fagei Boschma. Trophomeres each with a separate short stalk extending from the external part of the organ of fixation. Trophomeres with rather numerous (up to seven or eight) gonomeres, the latter of globular shape, not more than slightly longer than broad.

Amallocystis racemosus Coutière. Trophomeres each with a separate short stalk extending from the external part of the organ of fixation. Trophomeres with rather numerous (up to seven) gonomeres, the latter of oval shape, about twice as long as broad.

Amallocystis fasciatus Fage. Trophomeres in tufts of five or six, each tuft with a short stalk attached to the external part of the organ of fixation. Trophomeres with one, rarely with two or three gonomeres; the latter oval, twice as long as broad or slightly more elongated.

Amallocystis umbellatus n.sp. Trophomeres in tufts of ten to twenty, each tuft with a long stalk attached to the external part of the organ of fixation. Trophomeres with two or three (usually three) gonomeres of globular or slightly oval shape.

Amallocystis capillosus Fage. Trophomeres with long thin stalks, each more or less separately originating from the external part of the organ of fixation. Trophomeres with one gonomere of cylindrical shape. Gonomeres twice as long as broad or still more elongate.

Coutière regarded the specimen mentioned by Bate, the parasite of *Pasiphaea cristata* Bate, as a representative of his species *Amallocystis racemosus*, parasitic on *Pasiphaea tarda* Kröyer. The two specimens, indeed, have much in common. Both show approximately the same number of trophomeres; they are attached to their hosts in approximately the same spot (Bate's specimen on the second abdominal segment, Coutière's specimen on the third). The number of gonomeres occurring on the trophomeres, however, is different in the two specimens. In Bate's specimen in both of his drawings (Bate, 1888, pl. cxl, figs. 3, 3′) the trophomeres invariably bear three gonomeres, whilst in Coutière's specimen this number is variable, up to seven. It is, therefore, not altogether certain that the two parasites really belong to the same species.

The two specimens of *Amallocystis umbellatus* are slightly different. The specimen on *Hoplophorus grimaldii* Coutière has a far greater number of trophomeres than the one on *H. novae-zeelandiae* De Man, though this difference certainly does not point to a specific difference of the two. The host of the larger specimen is about twice the size of the host of the smaller specimen, which may be the reason for the more luxuriant development of the larger specimen. Further, it is not impossible that the smaller specimen had not yet reached its full size. It is of minor importance that the diameter of the trophomeres and the gonomeres in the smaller specimen is smaller than that found in the larger specimen.

Differences of this kind are of common occurrence in the various specimens of *Amallocystis fagei*. In connexion with the size of the host this species shows a strong variation in the number of the

trophomeres and in the dimensions of the trophomeres and the gonomeres. Gonomeres of small specimens may be less than half as long and broad as those of large specimens. The measurements of specimens on *Thysanoessa* from Icelandic waters were taken from the figures in Einarsson's paper (1945, fig. 83*b*, *c*). If these measurements (0·1 mm.) are correct the trophomeres and gonomeres of these Icelandic specimens are still smaller than those of the parasites on *Thysanoessa* from the Antarctic (0·13–0·16 mm.). For the present it must remain undecided whether the Arctic form really is specifically the same as the Antarctic form. The available data point to a specific unity.

The specimens of *Amallocystis capillosus* dealt with in the present paper correspond in all important characters with the specimens described by Fage. The trophomeres and gonomeres have the same shape and approximately the same dimensions. It is interesting that the specimen described in detail in the present paper pierces one side of the base of the rostrum of its host in two separate places. Undoubtedly normally there is one of these holes only at each side of the rostrum, as in the specimens described by Fage.

THE GENERA OF THE FAMILY ELLOBIOPSIDAE

The data obtained in the examination of the three species of the genus *Amallocystis* dealt with in the present paper give occasion for a comparison of these results with the data in the literature concerning the other genera of the Ellobiopsidae. The most striking fact presenting itself is the similarity of the genera *Ellobiopsis* and *Amallocystis*. With these two the genus *Rhizellobiopsis* seems to form one group. The comparatively little-known genus *Ellobiocystis* appears to be rather distinct from the group of three genera mentioned above, and the genus *Parallobiopsis* differs sufficiently from all the other genera of the family for it to be regarded it as a distinct group by itself. The arguments for this division of the family into different groups may be set forth in more detail.

In fully developed specimens of *Ellobiopsis chattoni* the external part may have a length of 700μ and a transverse diameter of 350μ. Then the pear-shaped external part is divided into a smaller trophomere and a larger gonomere (Caullery, 1910; Jepps, 1937), the gonomere being about twice as long as the trophomere, or having at least twice the volume of the trophomere. The parasite is attached to one of the anterior appendages of its host by a distinct organ of fixation which as a strong rod penetrates into the appendage. Apparently it is not only an organ of fixation but has also the function of absorbing the food.

The specimen of *E. chattoni* described and figured by Steuer (1928, 1932*b*, 1933), and regarded by him as an adult stage, shows a large pear-shaped trophomere capped by a much smaller globular gonomere, the length of the trophomere being 311μ, that of the gonomere 111μ. Moreover, in Steuer's specimen the groove between the gonomere and the trophomere is much more pronounced than in Caullery's specimens. The specimens figured by Apstein (1911) and by Willey (1920) show a small gonomere separated by a distinct groove from the much larger trophomere; in these respects they correspond with Steuer's specimen. The differences between the two forms possibly point to a specific distinction. For the present this must remain undecided.

An undoubtedly specifically separate form is *E. elongata* Steuer (1932*a*). When fully developed it consists of a cylindrical trophomere with a length of 250μ, and at the top of this trophomere are two globular gonomeres with a diameter of 70–80μ. Besides being much smaller than *E. chattoni* this parasite is distinguished by its peculiar shape. As in *E. chattoni* the stalk penetrates into the appendage of the host as a long thin organ of fixation.

The external part of *E. chattoni*, and even more distinctly that of *E. elongata*, closely corresponds with one of the external excrescences of the species of the genus *Amallocystis*. Principally *Amallocystis* is nothing but a compound *Ellobiopsis*, in which the organ of fixation has become more complicated

to ensure a strong fixation into the host and to develop into a strongly divided organ for the absorption of the food.

Amallocystis fagei, the species with the comparatively small number of trophomeres, is of a much more simple structure than the other species of the genus. The more or less complicated structure of the latter can be easily explained as modifications of the organization of *A. fagei*.

Rhizellobiopsis, the genus established by Hovassse (1926) for the parasite of the Annelid *Nephthys ciliata*, described by Zachs (1923) as *Ellobiopsis* (?) *eupraxiae*, is very similar to *Ellobiopsis*. The body consists of a rather large trophomere and a number of gonomeres (four in Zachs's figure). The distal gonomere in the figured specimen shows a kind of sporulation reminiscent of that described by Jepps (1937) in *E. chattoni*. *Rhizellobiopsis* differs from *Ellobiopsis* by its more or less dichotomously divided root system, but in other respects it has a strong resemblance to the species of *Ellobiopsis*, especially to *E. elongata*, in which two gonomeres develop on the top of the gonomere.

Of the various species described by Coutière (1911*c*) in his genus *Ellobiocystis*, very little is known besides their external shape. It seems to be certain that all these forms are simply attached to the cuticle of their hosts without penetrating into it. They are, therefore, no real parasites, but appear to lead a saprophytic mode of life.

Parallobiopsis coutieri Collin, which has been the subject of extensive studies by Hovasse (1926), is an organism which differs in many respects from *Ellobiopsis* and from *Amallocystis*. This parasite is attached to the cuticle of its host by a well-developed sucker. In the central part of this sucker the cuticle of the host is pierced, and here a protoplasmatic excrescence of the parasite penetrates into the tissues, thereby forming an organ for the absorption of food. The body of the parasite is divided by transverse septa into up to eight or nine divisions, the basal of which is the trophomere. At the top of the latter there are a few flat recently formed young gonomeres. Towards the free extremity the gonomeres gradually become larger, so that the distal gonomere is longer than broad.

Various opinions have been expressed concerning the place of the Ellobiopsidae in the classification of the Protozoa. Caullery (1910) was inclined to regard his genus *Ellobiopsis* as a parasitic Peridinean, and with some doubt it is included in this group in Chatton's (1920) monograph of the parasitic Peridinea. After Hovasse (1925*a*) had found that the spores of *Parallobiopsis* are flagellispores, he advocated the view that the Ellobiopsidae form a specialized group of the Flagellata. Afterwards also Steuer classified the Ellobiopsidae among the Flagellata. An entirely different view was expressed by Jepps (1937, p. 642): 'the information at present available seems to me to suggest a fungus relationship rather than any other—although perhaps such speculation is at present unprofitable.'

In the present paper no results are given of cytological details which might point to the affinities of the Ellobiopsidae with other groups of organisms. The particulars referred to above, however, might indicate that the genera which now are included in the family Ellobiopsidae do not form an altogether homogeneous group. It seems probable that especially *Parallobiopsis* is very little allied to *Ellobiopsis* and *Amallocystis*, and, consequently, when it is a fact that *Parallobiopsis* belongs to the Flagellata it is not yet certain that *Ellobiopsis* and *Amallocystis* too must be regarded as Flagellates. As long as no particulars concerning the sporulation of the last-named genera of more definite value than those at present available become known, no distinct indications in regard to their systematic position can be put forward.

GEOGRAPHICAL DISTRIBUTION OF THE ELLOBIOPSIDAE

In its typical form *Ellobiopsis chattoni* Caullery was once collected at Banyuls-sur-mer in the Mediterranean, and on several occasions in the region of the Firth of Clyde. If really all the parasites of this genus consisting of one trophomere with one gonomere which were described or mentioned by various

authors belong to *E. chattoni*, the species has a more or less world-wide distribution, as shown on the map in Steuer's (1932*b*) paper. *E. elongata* Steuer is known from one locality only, in the South Atlantic in the South Georgia region.

The specimens belonging to the genus *Ellobiocystis* were all collected in the region from the Bay of Biscay to the Azores. *Parallobiopsis* is known from the Mediterranean coastal waters of France only. *Rhizellobiopsis* was found in the material of two stations of the expedition of Prof. Deruguine in the White Sea. These seemingly restricted areas probably do not constitute the real regions of distribution of the genera mentioned here.

The available data concerning the distribution of the compound Ellobiopsidae seem to point to the fact that all these are of world-wide occurrence.

Amallocystis racemosus (Coutière) was found in the region to the north-east of Iceland. The Ellobiopsid mentioned and figured by Bate, and regarded by Coutière as belonging to *A. racemosus*, came from the region of the Fiji Islands.

A. fasciatus Fage is known from the Pacific (off New Zealand and the Fiji Islands), from the Atlantic, and from the Indian Ocean.

A. capillosus Fage is known to occur in the Skagerrak (Fage, 1938) and in the Strait of Magellan (specimens dealt with in the present paper).

The two specimens of *A. umbellatus* n.sp. are both from the Atlantic, one from the tropical region, east of Brazil, the other from the South Atlantic, west of Capetown.

The specimens of *A. fagei* Boschma dealt with in the present paper were all collected in the southern hemisphere and mostly in the Antarctic region. Some of them are from the South Atlantic: off South Brazil (St. 712), off Patagonia (St. WS 770), and Scotia Sea and off South Georgia (St. 665, 748, 751, 766, 1056). Others are from the South Pacific: Bellingshausen Sea (St. 733), and about half-way between New Zealand and Tierra del Fuego (St. 963, 965). Others again are from the South Indian Ocean: south of Australia (St. 892), and south-west of Australia (St. 869, 871, 872). *Amallocystis* sp., reported upon by Einarsson (1945), occurring in the waters around Iceland, in all probability belongs to *A. fagei*. It is probable that the specimen mentioned by Macdonald (1927) from Cumbrae Deep in the Firth of Clyde also belonged to the same species. This species then would also have a large area of distribution.

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PLATE XXXVIII

Amallocystis fagei Boschma

Figs. 1–3. Specimens on *Euphausia vallentini* Stebbing from St. WS 770. Side view of host. ×6.

Fig. 4. Specimen of fig. 1. Dorsal view of host. ×6.

Fig. 5. Specimen of fig. 2. Dorsal view of host. ×6.

Fig. 6. Specimen on *Euphausia recurva* H. J. Hansen from St. 712. Side view of host. ×6.

Fig. 7. Specimen on *Thysanoessa gregaria* G. O. Sars from St. 965. Side view of host. ×6.

Fig. 8. Specimen on *Euphausia frigida* H. J. Hansen from St. 751. Side view of host. ×6.

Fig. 9. Specimen on *Euphausia hemigibba* H. J. Hansen from St. 872. Side view of host. ×6.

Fig. 10. Specimen of fig. 2. ×21.

Fig. 11. Specimen of fig. 8. ×21.

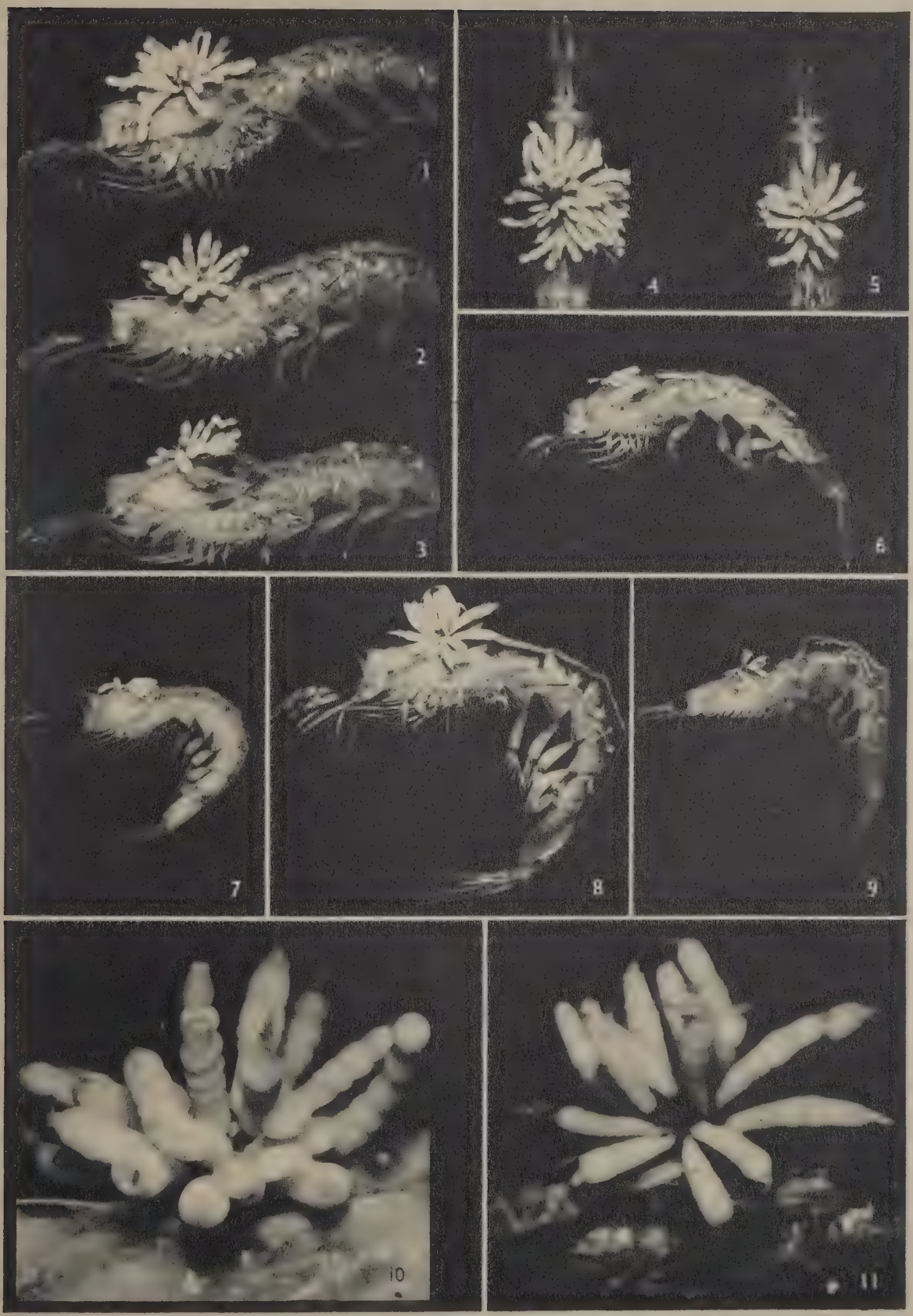
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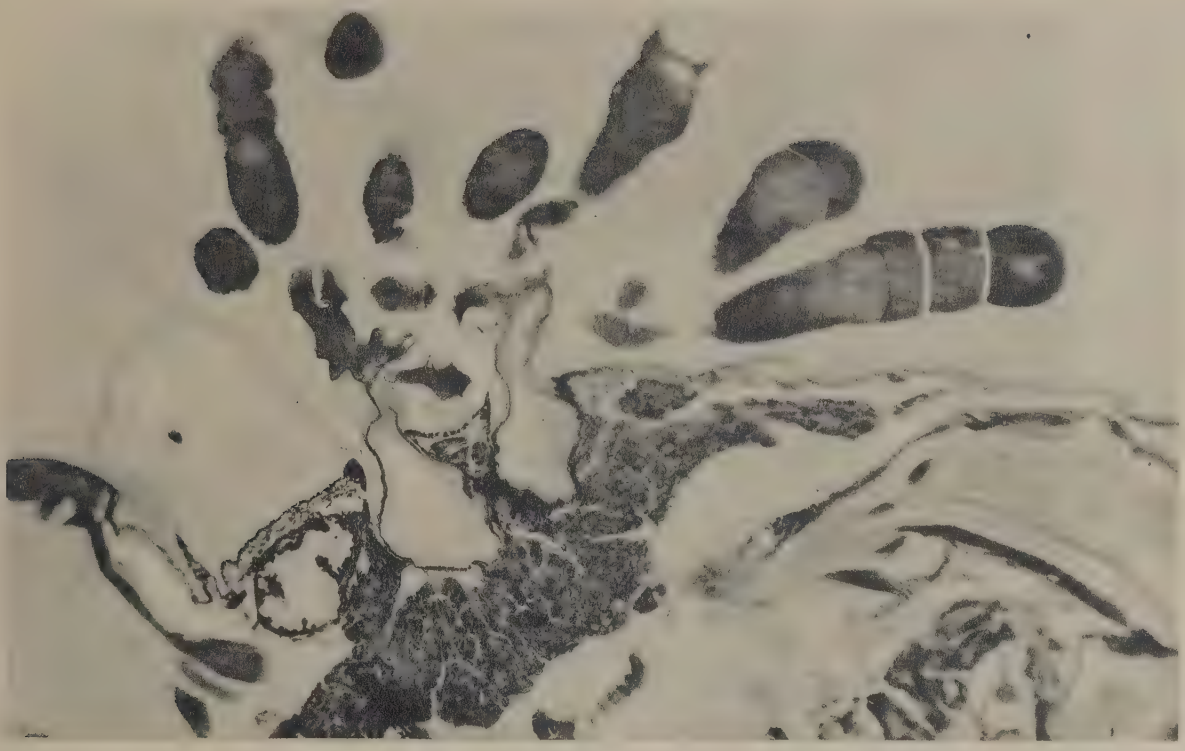
PLATE XXXIX

Transverse section of *Euphausia vallentini* Stebbing with *Amallocystis fagei* Boschma from St. WS 770. *a*, appendages of host; *f*, organ of fixation; *g*, gonomere; *h*, hepatopancreas of host; *i*, intestine of host; *m*, musculature of host; *n*, ventral nerve cord of host; *o*, ovary of host; *p*, protoplasmatic excrescences; *s*, sieve plate; *t*, trophomere. × 50.

PLATE XL

Upper figure: longitudinal section of *Euphausia vallentini* Stebbing with two specimens of *Amallocystis fagei* Boschma from St. WS 770. ×61.

Lower figure: Part of next section of the same specimen. ×525. *c*, cuticle of host; *e f*, external part of organ of fixation; *f*, organ of fixation; *g*, gonomere; *h*, hepatopancreas of host; *ht*, heart of host; *m*, musculature of host; *o*, ovary of host; *p*, protoplasmatic excrescences; *s*, sieve plate; *st*, stomach of host; *t*, trophomere.



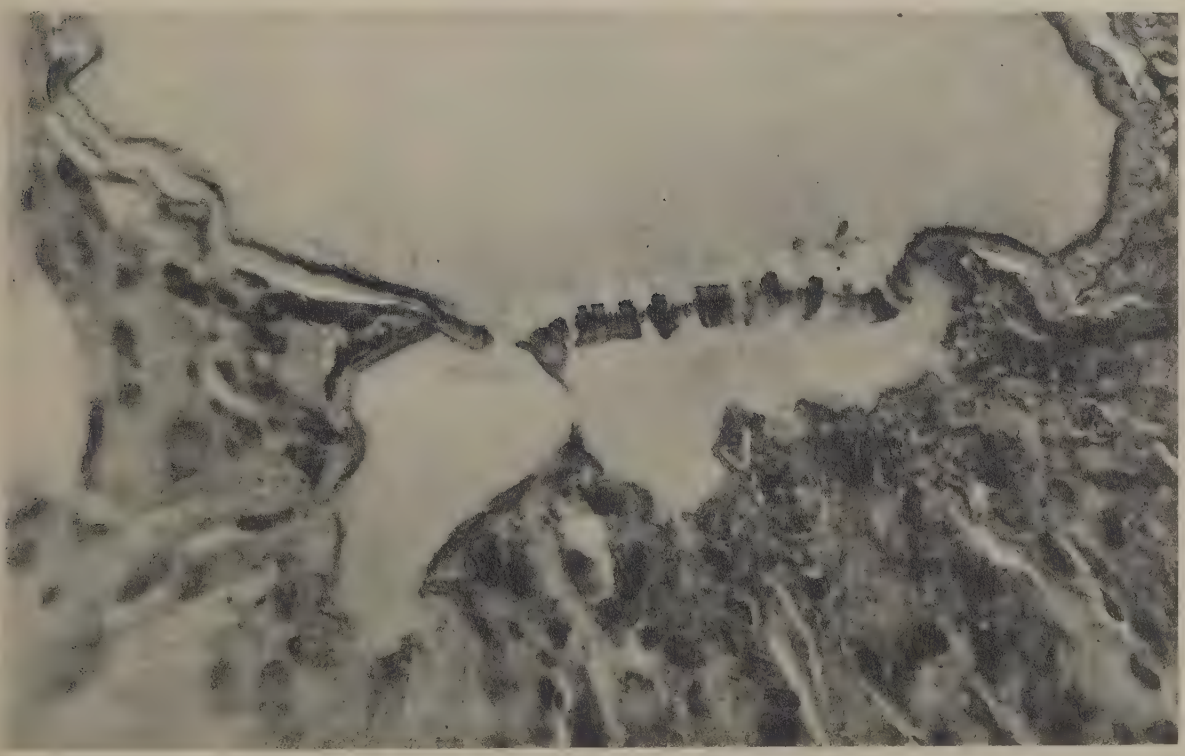


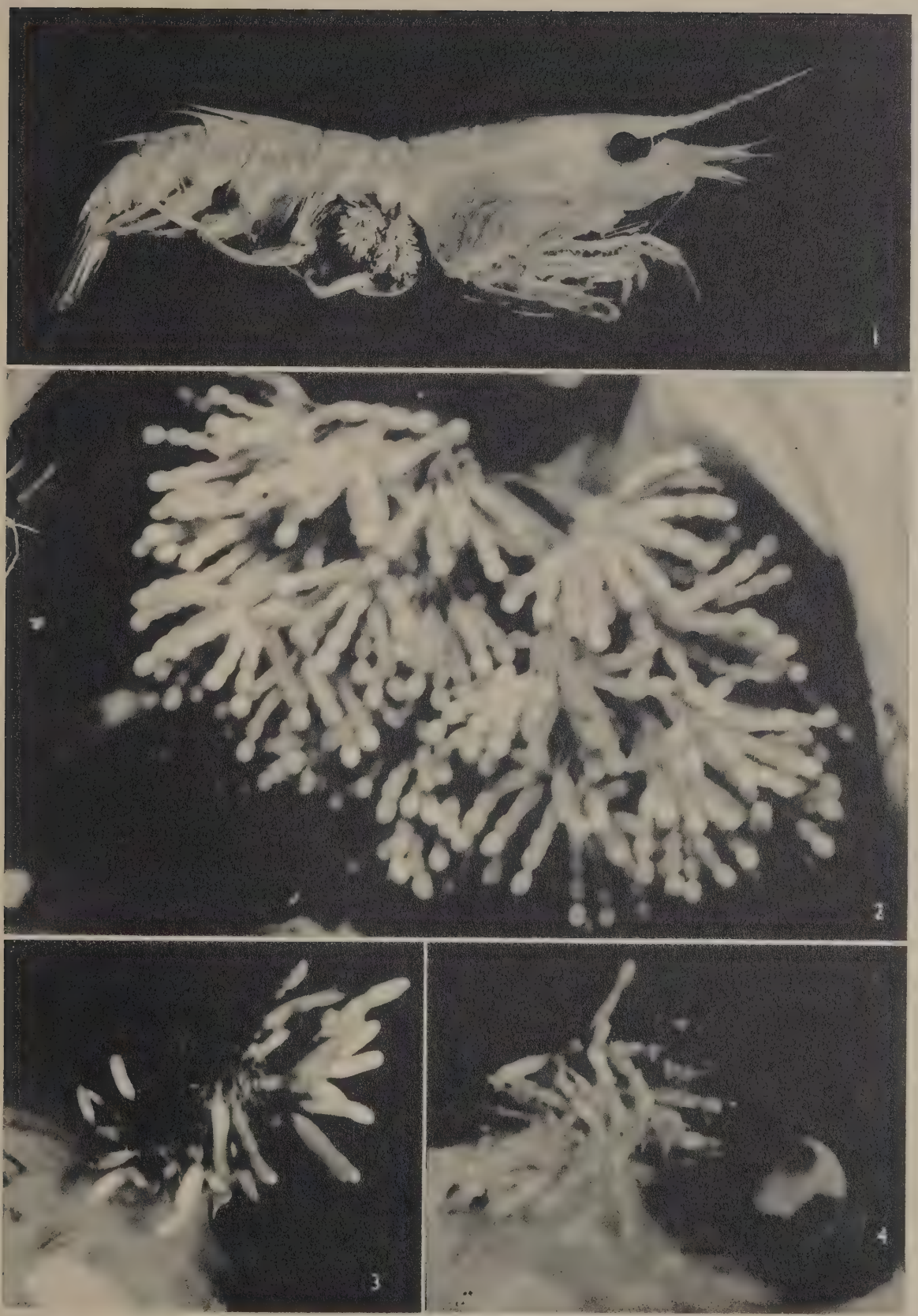
PLATE XLI

Fig. 1. *Hoplophorus grimaldii* Coutière with *Amallocystis umbellatus* n.sp. Slightly more than × 2.

Fig. 2. *Amallocystis umbellatus* n.sp. Same specimen. × 18.

Fig. 3. Rostral region of *Pasiphaea acutifrons* Bate with *Amallocystis capillosus* Fage. Approximately × 14.

Fig. 4. Rostral region of *Pasiphaea acutifrons* Bate with *Amallocystis capillosus* Fage. Sectioned specimen. Approximately × 14.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